



KALMIOPSIS

Journal of the Native Plant Society of Oregon

OREGON PLANTS, OREGON PLACES

A new feature of KALMIOPSIS, page 21



Bridge Creek Valley, Wheeler County near Painted Hills — 1889

KALMIOPSIS

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EDITORIAL

Next time you are in north central Oregon, stop by the Painted Hills Unit of the John Day Fossil Beds National Monument. Take along this volume of KALMIOPSIS. We hope our new feature, **Oregon Plants, Oregon Places**, makes your trip a little more enjoyable.

We celebrate Bradshaw's desert-parsley as KALMIOPSIS' Plant of the Year. Plain, rare, and under assault, *Lomatium bradshawii* is Oregon's third species to be placed under the protection of the Endangered Species Act. KALMIOPSIS commends the efforts of all who are working diligently to preserve what is left of our natural heritage.

These are times when it is easy to imagine we are in the midst of an extinction event unparalleled since the close of the Cretaceous. Then, an asteroid likely caused the loss of species. Today, the asteroids are us, members of the human race. We all actively or passively contribute, each of us in different ways. Try to find a way to make a difference.

Native Plant Society of Oregon

The Native Plant Society of Oregon is an organization of lay and professional botanists interested in Oregon flora. The work of the Society includes preservation of native flora and the botanical education of Society members and the public. The Society accomplishes the former goal by taking an active role in monitoring programs, by active participation in plant conservation issues, by helping establish botanical preserves and by protecting significant plant populations. We meet our educational goals through our local chapter meetings, field trips, and publications. The Society awards the Jean M. Davis Memorial Scholarship to students studying Oregon flora and awards several modest research grants yearly. Membership includes participation in local chapter meetings, field trips, and subscriptions to the BULLETIN and KALMIOPSIS (also available separately at \$5.00 per issue). The monthly BULLETIN includes notices of chapter meetings and activities, conservation issues and short articles of interest to the membership. KALMIOPSIS features longer articles of interest to lay and professional members of the Society.

Volunteers do the work of the Society. Money is raised by membership dues, and sale of posters, notecards, and tee shirts. Additional donations, bequests, and memorial gifts greatly help the Society in its efforts.

MEMBERSHIP

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THE COVER

Bridge Creek Valley in 1889. Photograph taken by the Princeton University Paleontologic Expedition. See **Oregon Plants, Oregon Places**, page 21.

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Bradshaw's Desert-Parsley: Population Monitoring and Pollination Biology¹

By Thomas N. Kaye



KAYE

Lomatium bradshawii (Bradshaw's desert-parsley) is unique. It is the only plant species in western Oregon listed by the US Fish and Wildlife Service as endangered. It is rare; only a handful of populations in remnant prairies and fence-rows are known, all in the Willamette Valley. And it is a challenge; conserving the species requires a thorough understanding of its biology. To preserve a species it is essential to know how it reproduces, what controls its population growth and decline and how to maintain an appropriate habitat (Harper, 1979; Massey and Whitson, 1980).

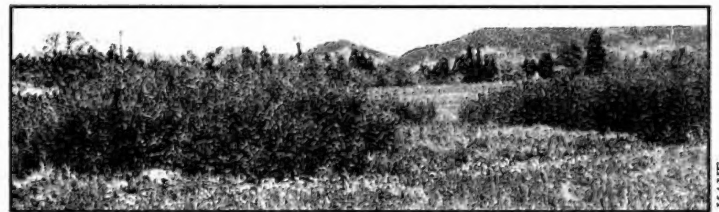
Thanks to the efforts of several researchers, a great deal of information on *L. bradshawii* is already known. In this article I report the results of my research on the pollination and population biology of *L. bradshawii* and review some work of others. Much of my work was conducted at a population in Buford Park east of Eugene near Mount Pisgah. This population met all the conditions necessary for the studies I conducted: It was easy to reach, occurred on public land, contained a large number of flowering plants, and botany students from nearby Lane Community College were able to participate in the study.

Monitoring the Buford Park Population

The population of *L. bradshawii* at Buford Park is at the eastern limit of the species' range, and is one of about a dozen populations known. When I first visited the site in the spring of 1990, it was obvious that the population was in jeopardy. I came to attend an on-site meeting of federal, state and county agency representatives with the purpose of evaluating the effect of cattle grazing on this sensitive plant and its habitat. *Lomatium bradshawii* plants had been trampled and eaten, the vegetation was grazed, and in some places, the soil was deeply churned by cow hooves. Cow flocks punctuated the scene. The meeting's participants

recommended that the area containing the population be fenced to exclude cattle, and thanks to a cooperative rancher, the fence was built a few months later.

Despite the negative impact of cattle that we observed, and that has been documented for other *Lomatium* species (e.g. Willoughby, 1987), grazing apparently had a role in maintaining the habitat for *L. bradshawii*. For hundreds or even thousands of years, Native Americans burned the prairies of the Willamette Valley, a practice that restricted the growth of woody vegetation and kept grasslands open. After settlement by Euro-Americans, fires were suppressed and trees and shrubs replaced large areas of native prairie (Johannessen et al., 1971). The cattle in Buford Park partially filled the role of fire by suppressing woody vegetation. Even with cows, however, large clumps of *Spiraea douglasii* grow in the wet-prairie habitat of *L. bradshawii*, and fire or manual cutting may be needed to maintain the open prairie the species seems to require. Connelly and Kauffman (1991) from Oregon State University have shown that *L. bradshawii* plants increase in size and seed production after their habitat is burned. Thus, fire may be the best tool to stimulate population growth and maintain the open prairie if the population declines.



KAYE

Spiraea encroaching into the wet desert-parsley habitat in the absence of fire choking out the prairie species.

Baseline information, updated annually, will help determine if and when the habitat at Buford Park should be burned or mowed. I decided to establish permanent transects for monitoring the *L. bradshawii* population to provide these data. With the help of Dr. Rhoda Love's botany class from Lane Community College, I established six transects in the population at Buford Park. At every meter along the transects, we mapped and measured each *L. bradshawii* plant in 20 x 50 cm plots. Some transects were placed in the open, while others were positioned near the expanding edge of *Spiraea* clumps to document the effect of shrub encroachment. Of course, after only one season of data collection, no trends can be reported. However, some patterns revealed by the structure of the population, especially when compared to other sites, are worth describing now. I sampled a population at Amazon Park in Eugene for detailed comparison with the Buford site.

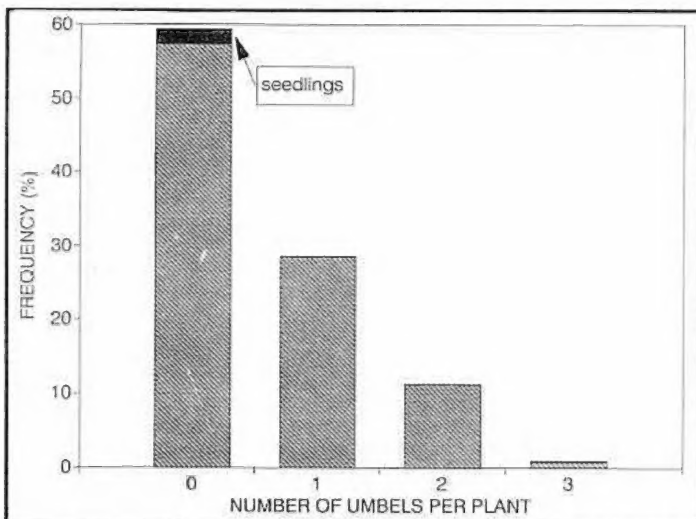
¹ A publication of the Restoration Ecology and Conservation Biology Cooperative Project (Oregon State University and Oregon Department of Agriculture).



Annual monitoring is necessary to determine if the population at Buford Park is declining because of shrub invasion. An enthusiastic botany class from Lane Community College helped with the 1991 sample.

Plant Size and Population Structure

The population at Buford Park was very dense, averaging 52 plants/m² with a maximum of 230 plants/m². This density was higher than any previously reported for *L. bradshawii*, including all the sites sampled by Connelly and Kauffman in 1988-1990, and the Amazon Park population. Also, the plants at Buford Park were relatively small, averaging only 16 cm tall with three leaves. Plants at other sites were generally taller with more than three leaves. My curiosity was piqued by NPSO member Tom Pringle who suggested to me that the fruits of *L. bradshawii* looked bigger at Amazon Park than at Buford. When I sampled the plants at Amazon Park I found that, in a population with a density of only 4 plants/m², the average plant produced 75 seeds on two umbels (flower clusters). But Buford plants matured an average of only 8 seeds on 1.2 umbels! Pringle was right; fruits from Amazon Park were nearly twice the length and weight of the Buford fruits. The small stature and low seed production of the Buford plants may have been related to high population density at that site. As density increased, leaf length, umbel number and plant height decreased significantly. One hypothesis to explain this pattern is that conditions for seedling establishment at Buford Park may be good, but soil nutrients may be limiting, thus leading to a high density of small plants. The situation may be reversed at Amazon Park, with plentiful nutrients and poor conditions for seedlings.



Seedlings made up only two percent of the population at Buford Park. Most individuals were non-reproductive.

Seedlings of *L. bradshawii*, however, were not very abundant at Buford Park in 1991. Only 2% of the individuals mapped had the cotyledon leaves indicative of first-year plants. Reproductive plants made up about 40% of the population, while the remainder were non-flowering. Small plants tended to be seedlings or non-reproductive, while large plants usually produced flowers. In general, the Buford population was skewed toward small and non-reproductive plants, a structure similar to that reported by Connelly and Kauffman.

Pollination Biology

Lomatium bradshawii does not reproduce vegetatively (e.g., by runners or basal sprouts). Instead, it relies on seed production, and therefore pollination, for population maintenance. At first glance, the pollination biology of *L. bradshawii* appears simple. The flowers are presented in a flat-topped umbel that most insects, large or small, can visit and pollinate. Upon closer inspection, the breeding system is more complicated. *L. bradshawii* has two kinds of flowers, male (stamens only) and hermaphroditic (stamens and pistil). Only the latter type can produce fruits and seeds. As in most species of *Lomatium*, the hermaphroditic flowers are protogynous; i.e., the stigmas become receptive and exerted before the anthers shed their pollen. In addition, the first umbel on a given plant will have a majority of male flowers, while later umbels will have a higher proportion of hermaphroditic flowers (Schlessman, 1978, 1980).



In Bradshaw's desert-parsley only perfect flowers produce fruits. A swallow-tail butterfly caterpillar at Buford Park.

In his Master's thesis on the biology of *L. bradshawii*, Kagan (1980) showed that reproductive plants produced one or two (rarely three) umbels per season. The umbel is usually all male, and the second has at least some hermaphroditic flowers. Each phase of sexuality in *L. bradshawii* appears to be sequential. I observed that, on umbels with hermaphroditic flowers the hermaphrodites were usually on the outer umbellets, and on the outer edge of the outer umbellets. The outer umbellets and the outer flowers were always the first to bloom, resulting in protogyny. Although some self-pollination may occur (and *Lomatium* species are usually self-compatible), the probability of cross-pollination by insects is increased because male and hermaphroditic flowers within a single plant mature at different times. Pollination biologists consider this type of breeding system to be the result of natural selection for outcrossing, and thus gene flow, to offset the deleterious effects of inbreeding. Unfortunately, efforts thus far by Kagan and myself to test for self-pollination in *L. bradshawii* have failed for various reasons, and it is still unknown whether hermaphroditic flowers can set seed in the absence of insects.

Insect Visitors

Species that rely on insects for pollination are vulnerable to the loss of their pollinators, for without them, they are unable to produce seeds and new individuals. For example, an orchid species pollinated by a single species of long-tongued moth could die out if the moth became extinct. Although *L. bradshawii* may be capable of some self-pollination, the breeding system described above suggests that insect-mediated cross-pollination is the rule. Therefore, the fate of *L. bradshawii* may depend, at least in part, on the survival of its pollinators. The Willamette Valley is an intensely agricultural area. Every year a huge acreage, including many fence-rows and road-sides, is sprayed with insecticides and herbicides. Local destruction of pollinating insects and their nesting habitat is cause for concern. Does *L. bradshawii* depend on insect pollinators that could be damaged by this spraying? Researchers have suggested that rare plant populations should be surrounded by a no-spray zone with a three-mile radius to protect vital pollinators (Tepedino, 1990). However, very little is known about the pollinator(s) of *L. bradshawii*. Information on their identity and abundance may be crucial to the recovery of this endangered species.

In 1990 and 1991 I visited four populations of *L. bradshawii* to observe and collect insect pollinators for identification and examination of pollen load. These populations, Buford Park and Amazon Park in Lane County, and Finley National Wildlife Refuge and Jackson-Frazier wetland near Corvallis in Benton County, were chosen to represent the geographic range of the species. I worked during various weather conditions (sunny to rainy) and times of day. *Lomatium bradshawii* blooms in early spring, usually in April, before many insect species are active. Even so, I encountered a large variety of bees, flies and other insect visitors to the plants. In all, I collected 93 specimens representing 25 species from flowers of *L. bradshawii* (Table

1). Two extremely small species of flies did not carry pollen and were unlikely pollinators. Also, ants observed on umbels at the Jackson-Frazier population did not carry pollen, seldom moved among plants and were probably ineffective pollinators. However, ten species (bees, flies, wasps and beetles) carried pollen on their bodies or legs, demonstrating their potential ability to cross-pollinate *L. bradshawii*, and most insects frequently moved from one plant to another. At least one bee, in the genus *Andrena*, may be the same as that observed by Kagan in 1980. Hover-flies (family Syrphidae) were prominent among the flies observed in 1991.



A hover fly (Syrphidae, *Sphaerophoria* sp.) visits Bradshaw's desert-parsley.

One important pattern was that the relative abundance of bees and flies changed from 1990 to 1991. The 1990 collections were dominated by solitary bees, but flies outnumbered all other insects in 1991. Weather conditions may have been more suitable for bees (i.e. warmer) in 1990, and flies may have been better able to tolerate the cooler April of 1991. In addition, only three insect species were seen at more than one site. No single insect species dominated the pollinator fauna of *L. bradshawii* in two years of observations. Instead, a high diversity of insects visited the flowers, and many of these appeared capable of affecting cross pollination. Apparently, *L. bradshawii* is not vulnerable to population swings of any one insect species.

Conservation

The successful maintenance and recovery of *L. bradshawii* depends on an adequate understanding of the species' biology. Protecting the habitat of the species from develop-

ment is of foremost concern, but the dynamic nature of its interactions with the environment, plant succession, fire and insect pollinators require that we do more. Only a small part of the "story" of this species has been told in these pages. It is hoped that the combined knowledge of many researchers working on various aspects of the biology of *L. bradshawii* will allow us to protect it in perpetuity. Sooner or later the Buford Park population will require some rigorous management, such as burning to control shrub invasion. We now have the baseline information to help decide when that action should be taken. The complex breeding system of the species indicates that insects may be crucial to cross-pollination and seed production. Fortunately, floral visitors appear to be diverse and widely capable of pollinating the flowers. In the long-run, protecting the nesting sites of pollinators may be a necessary component of the species' conservation.

TABLE 1. Insect visitors to *Lomatium bradshawii* flowers at four sites in the Willamette Valley in 1990 and 1991. Numbers indicate how many specimens of each taxon were collected. The family is given when the genus is unknown.

	Buford 1990	Buford 1991	Finley 1990	Finley 1991	JF 1991	Amazon 1991
Solitary Bees						
<i>Andrena</i> sp. 1*	7					
<i>Andrena</i> sp. 2*	1					
<i>Ceratina</i> sp.			5			
Halictidae sp.					1	
<i>Lasioglossum</i> sp.			1		1	
<i>Melanostoma</i> sp.*				1		
Tenthredinidae sp.*				1		
Wasps						
Ichneumonidae sp.*				1		
Flies						
Anthomyiidae sp.		1		5	1	
Calophoridae	1					
<i>Cheilosia</i> sp.		1				
Empididae sp. 1		3			5	6
Empididae sp. 2**				3		
<i>Mesograpta marginata</i> *	1					
<i>Paragus</i> sp.*					18	
<i>Rhagio</i> sp.						1
<i>Sphaerophoria</i> sp.*					5	
<i>Xylota</i> sp.*	1					
Misc. Diptera**	1					
Caddisflies						
Trichoptera sp.						2
Beetles						
<i>Bruchus brachiodis</i>						1
<i>Dalopius</i> sp.						1
<i>Diabrotica</i>						
undecimpunctata				1		
<i>Lebia moesta</i> *					5	
Ants						
<i>Formica fusca</i> *					1	
Total specimens	12	5	6	12	47	11
Total species	6	3	2	6	7	5
Bees/Flies/Other	66/33/0	0/100/0	100/0/0	17/67/8	4/63/11	0/64/36

*specimens carried pollen.

**individuals very small and unlikely to transfer pollen among umbels.

Acknowledgements

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F. Lang, R. Love, R. Meinke, W. Messinger and M. Wilson. I owe many thanks to Rhoda Love and her botany class from Lane Community College for assisting with the monitoring at Buford Park. Rick Westcott from the Oregon Department of Agriculture and Wes Messinger from OSU identified the insects. Field work in 1991 was funded by a research grant from the Native Plant Society of Oregon.

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Evolution Before Darwin: The Musings of Constantine Rafinesque

By Kenton L. Chambers



Constantine Rafinesque

JOHN MEGAN

In the history of biology, Constantine Rafinesque (1783-1840) and Charles Darwin (1809-1882) represent what are probably polar opposites among 19th century naturalists. Both were true intellectual geniuses, exceptionally broad in their knowledge and interests; both wrote prolifically; both took their initial inspiration from the science of taxonomy — the naming and cataloging of biological diversity; and both were famed as explorers of the untamed wilderness. However, they could not have been more unlike in their intellectual approach to science, nor the impact of their research on contemporary and future biological thought.

Rafinesque is in many ways a unique character in the annals of North American natural history. His name is given brief, if any, mention in modern encyclopedias and biographical dictionaries of science and scientists. Peattie (1936) called him "the most widely celebrated unknown man in science, equaling in brilliant obscurity Roger Bacon or Paracelsus." Born in Constantinople of European parents, educated in Italy and France, Rafinesque emigrated to the then-youthful United States in 1802, searching for fame and fortune. Neither wealthy nor aristocratic, he

lived off the generosity of his friends and patrons; what money he accumulated was spent to finance his travels and publications. He resided at various times in New York and Philadelphia, meeting and corresponding with nearly all the well-known scientists of the period. The only academic position he held was between 1819 and 1826, at Transylvania University in Lexington, Kentucky, described by Peattie (1936) as "a backwoods Oxford." The taming of the American West had begun, and Rafinesque was there to explore far and wide for new species of plants and animals. Geology, botany, mammology, herpetology, conchology, prehistoric Indian mounds, fossil Ice Age animals and the languages of Native Americans all attracted his attention. He wrote voluminously on every subject imaginable. Students at the university thought of him as "a man of peculiar habits and... very scientific... his room in the College [was] filled with butterflies and bugs and all sorts of queer things" (Call, 1895). It was said that he never went on a field expedition without carrying along his trusty umbrella (good advice for Oregon botanists, as well)!

The scientific passion of Rafinesque's life was natural history, a dominating field of biology in those days. The sublime goal of natural history was to discover, describe and name the "works of nature" in all their glorious diversity. The course of 18th century biology had already been shaped by Rafinesque's predecessor Carl Linnaeus (1707-1778), the pre-eminent figure in Swedish science. By his energy and genius, this man had single-handedly initiated the science of taxonomy in its modern form. Linnaeus established for Rafinesque, and for the whole of Western (European-dominated) science, an inspiring intellectual goal — to develop a classification system for all of nature. During this historical Age of Exploration, when European power and civilization were spreading to every corner of the globe, it was assumed that human rationality could finally discover the pure order of nature. The secret of life was in the relationships of living organisms. By discovering the pattern of life, humankind could hope to discern the very mind and purpose of the Creator. Small wonder, then, that from such a perspective the followers of Linnaeus would devote their lives to discovering and naming the entire earth's flora and fauna.

In Rafinesque's case, the devotion to science was there but the rewards were not. Merrill (1949) remarked, "It is doubted if in the entire history of descriptive biology there is any other author who has suffered more from the weight of authority... The leading biologists of his time, both in Europe and in America, ignored his numerous nomenclatural proposals to an extraordinary degree, whether he was correct in his conclusions or not." Yet he was a prolific author, with a bibliography of over 1,000 published books and articles! In botany alone, he proposed nearly 2,700 new

generic names (Merrill, 1949), yet only about 30 of these are in use today. The rest have either been relegated to synonymy (i.e., the genus involved had already been named by a taxonomist prior to Rafinesque); or in cases where he was truly the first to name various accepted genera, Rafinesque's proposed names have been officially "rejected" in favor of later-published generic names.

Rejection of over 90 Rafinesquian generic names occurred by action of International Botanical Congresses early in the 20th century, but it was indirectly due to the neglect of Rafinesque's work by his contemporaries in the 1800's. The belated discovery of his taxonomic proposals (buried, as they were, in his 1,000-plus obscure publications) meant that too many well-known plant names would have to be changed; so the botanists voted simply to reject — that is, ignore — much of his pioneering work. Some Oregon genera that were named first by Rafinesque but are now called something else are: *Camassia* (*Cyanotris* Raf.), *Castanopsis* (*Balanoplis* Raf.), *Chlorogalum* (*Laothoe* Raf.), *Chrysopsis* (*Diplogon* Raf.), *Hesperochiron* (*Capnorea* Raf.), *Lithophragma* (*Pleurendotria* Raf.), *Piptochaetium* (*Podopogon* Raf.), *Stenanthium* (*Anepsa* Raf.), *Stephanomeria* (*Ptiloria* Raf.), and *Suksdorfia* (*Hemieva* Raf.). On the other hand, a check of Peck's **Manual of the Higher Plants of Oregon** (1961) turned up the following names by Rafinesque which we do recognize and use: *Agoseris* (*Asteraceae*); *Clintonia* (*Liliaceae*); *Cymopterus*, *Lomatium*, *Osmorhiza*, and *Oxypolis* (*Apiaceae*); *Distichlis* and *Sitanion* (*Poaceae*); *Olsynium* (*Iridaceae*); *Paxistima* (*Celastraceae*); and *Polanisia* (*Capridaceae*).

In comparing the relative influence of Charles Darwin and Constantine Rafinesque on the history of biological thought, we can see how certain personal characteristics of the two men played a dominant role. Rafinesque's intellect was impatient and flighty, revealing its genius in breadth of knowledge but not in depth. His mind roamed freely through the sciences of his day — anthropology, archeology, botany, entomology, geology, history, linguistics, medicine, meteorology, paleontology and zoology. But his writings appear to be almost totally unorganized; they skip from subject to subject, with ideas, observations and theories all thrown together willy-nilly. Rafinesque seemed incapable of ever settling on a single theory or subject and studying it in convincing detail. His reputation among fellow naturalists of the early 1800's was that of a crank and crackpot. Nobody felt it was worth the trouble to sift the wheat from the chaff in Rafinesque's voluminous writings. In fact, he was ridiculed for his almost insane compulsion

to name and rename every plant and animal as "new to science;" his publications and ideas were simply ignored.

Darwin, as is well known, received the wholehearted approval and respect of his scientific contemporaries. Although personally modest and retiring, he possessed a disciplined and penetrating intellect along with an unsurpassed ability to deduce general principles from diverse facts and observations. In 1876, Darwin wrote of himself (Darwin, 1892): "My mind seems to have become a kind of machine for grinding general laws out of large collections of facts." Instead of wasting his mental powers, as Rafinesque did, Darwin concentrated his efforts on marshalling evidence for his two great discoveries — organic evolution and natural selection — and on presenting a case so convincing that it initiated a revolution in biological thought.

In his autobiography, Darwin states that it was "about 1839" when he "clearly conceived" his theory of evolution by means of natural selection. His famous book **On the Origin of Species...** (Darwin, 1859) was published 20 years later. Historians have made much of the fact that glimmerings of evolutionary theory can be found in writings of various pre-Darwinian naturalists — for example, George Louis Buffon, Jean Baptiste Lamarck and Charles's grandfather, Erasmus Darwin (Eiseley, 1958). In hindsight, and with our knowledge that Darwin's basic premises concerning evolution have been abundantly confirmed by over 130 years of biological research, it is indeed interesting to read the words of these earlier biologists whose theories never "caught on" as Darwin's did. Peattie (1936) wrote that Darwin's great advantage was timeliness and "publicity." He expressed it this way (p. 158): "Careful looking has shown that Darwin had about a hundred fore-runners. In all ages and in all languages sages have tried to put over the concept of evolution. They found no takers until the angelic origin of man himself was assaulted; the storm that this created in Victorian England gave the concept all that an idea, be it a Red Cross drive or a California cult, requires for success. That is publicity." Beyond this, however, I believe that Darwin succeeded because he not only produced a brilliant theory, but also a convincing mechanism — natural selection — by which biologists could conceive of "how it happened" as well as "what did happen" during the history of life.

Rafinesque's evolutionary musings, as I call them, appear in a characteristically brief and unadorned note, occupying less than two columns of type, in the 1833 spring issue of a periodical entitled "Atlantic Journal and Friend of



Rafinesque named *Clintonia* for DeWitt Clinton, Erie Canal builder, governor of New York, and naturalist. Our queen's cup and saucer lily, *C. uniflora*, graces moist conifer woodlands in the mountains. FAL



Rafinesque switched *Pachystima*, *Pachistima*, and now *Paxistima* (see page 16), from the holly genus *Ilex*. Loved by Oregonians as Oregon boxwood, professional collectors eagerly seek its hardy evergreen foliage for the florist's trade. FAL



Our beautiful purple-eyed grass or grass-widows grows best in soil pockets on rocky slopes and flats. We must become accustomed to its new name, *Olsynium douglasii*, another of Rafinesque's genera, and not *Sisyrinchium douglasii* (see page 17). FAL

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organs, taking place in the lapse of time. There is a tendency to deviations and mutations through plants and animals by gradual steps at remote irregular periods. This is a part of the great universal law of PERPETUAL MUTABILITY in every thing.

Thus it is needless to dispute and differ about new G. Sp. and varieties. Every variety is a deviation which becomes a Sp. as soon as it is permanent by reproduction. Deviations in essential organs may thus gradually become N. G. Yet every deviation in form ought to have a peculiar name, it is better to have only a generic and specific name for it than 4 when deemed a variety. It is not impossible to ascertain the primitive Sp. that have produced all the actual; many means exist to ascertain it: history, locality, abundance, &c. This view of the subject will settle botany and zoology in a new

way and greatly simplify those sciences. The races, breeds or varieties of men, monkeys, dogs, roses, apples, wheat,... and almost every other genus, may be reduced to one or a few primitive Sp. yet admit of several actual Sp. names may and will multiply as they do in geography and history by time and changes, but they will be reducible to a better classification by a kind of genealogical order or tables.

My last work on Botany if I live and after publishing all my N. Sp. will be on this, and the reduction of our Flora from 8000 to 1200 or 1500 primitive Sp. with genealogical tables of the gradual deviations having formed our actual Sp. If I cannot perform this, give me credit for it, and do it yourself upon the plan that I trace.

C. S. R.

124. Principles of the Philosophy of new Genera and new species of Plants and Animals.

Extract of a letter to Dr. J. Torrey of New York dated 1st Dec. 1832.... I shall soon come out with my avowed principles about G. and Sp. partly announced 1814 in my principles of Somiology, and which my experience and researches ever since have confirmed. The truth is that *Species and perhaps Genera also, are forming in organized beings by gradual deviations of shapes, forms and*

Knowledge." This peculiar journal was written and financed entirely by Rafinesque himself and consisted of 212 pages in eight parts, issued during 1832 and 1833, and offered for sale at a price of two dollars! The subtitle given in Volume I, Number I, well illustrates the grandiose plans that Rafinesque had for his journal: "A Cyclopedic Journal and Review of Universal Science and Knowledge: Historical, Natural, and Medical Arts and Sciences: Industry, Agriculture, Education, and Every Useful Information: with Numerous Figures." The article in question appears on pp. 163 and 164, with the title: "Principles of the Philosophy of New Genera and New Species of Plants and Animals." Rafinesque states that it is an extract of a letter which he wrote to Dr. John Torrey (1796-1873), a leading American botanist of the time, on December 1, 1832. Presumably Torrey frequently received letters from Rafinesque on botanical matters, but whether he paid any attention to this particular one is not known. Like his close colleague Asa Gray (1810-1888) of Harvard University, Torrey probably had no notions of evolution, prior to the popularization of the subject by Darwin (1859).

Let us examine some of the ideas expressed by Rafinesque in his 1833 publication. (The terms "G." and "Sp." in line 3 stand for *genera* and *species*. Rafinesque coined the term somiology to mean the science of classification both in theory and practice. However, A.P. de Candolle introduced the widely used term taxonomy for this branch of science a few years earlier.) Rafinesque stated his opinion that species and genera are not fixed and permanent; rather, they develop and change gradually through time. He even used the word "mutations," which is a key principle in the modern genetic explanation of evolution. His words "by gradual steps at remote irregular periods" can be read to mean he appreciated the great amount of time required for evolutionary change, and he sensed there had been past changes in the rate of evolution; i.e., that periods of more rapid change alternated with periods of slow change. A concept quite similar to this is now explicit in evolutionary theory; namely, the idea of "punctuated equilibrium" (Gould and Eldredge, 1977). Also, it is now accepted that earlier periods of evolutionary stasis coincide with stable, long-persistent environmental conditions, whereas bursts of evolutionary change in organisms occur after catastrophic environmental disruptions of various kinds (particular attention having been given to the impact on the earth of one or more asteroids/comets 65 million years ago, when dinosaurs and many other animal groups became extinct).

In the second paragraph, Rafinesque states "Every variety is a deviation which becomes a Sp. [species] as soon as it is permanent by reproduction." This principle was basic to Darwin's thinking, as well; in modern terms, it refers to the so-called "biological species concept," which despite many exceptions is a widely used definition of species today. In a "biological species" (really a "genetic species") any given individual is potentially capable of mating with any individual of the opposite sex; however, members of different species are expected to be unable to interbreed. In these terms, each natural species is "permanent by reproduction," as Rafinesque says. Most 19th century naturalists, including Rafinesque and Darwin, were well

aware of the many domestic breeds of animals and cultivated varieties of plants that had been produced by agricultural breeding and selection throughout human history. In his writings on evolution, Darwin (1868) made good use of the analogy between such domesticated types, which are "true-breeding" due to human selection, and naturally-occurring varieties and races which may become true-breeding new species through the workings of natural selection. Studies of evolution today go far beyond these early ideas. Formation of new species through divergence of evolutionary lineages is called "speciation." Knowledge of speciation processes derives from studies of population genetics, differing modes of reproduction (including inbreeding, outcrossing, asexual propagation), isolating mechanisms (e.g., genetic, chromosomal, ecological, behavioral, geographical), hybridization and mathematical models for the evolutionary effects of mutation rates and selection coefficients.

"Deviations in essential organs may thus gradually become N.G. [new general]," says Rafinesque. To him, essential organs were those of the flowers and fruits; in a later work (Rafinesque, 1836, p. 18) he wrote: "Genera are the groups of species that have similar floral characters and sometimes a similar habit. Whenever a species has different floral forms it must be a peculiar genus." He himself had noted many such "deviations" (Rafinesque, 1836, p. 16), such as "in a garden a Tulip with 5 petals only and 5 stamens," "a *Tecoma* [note: a vine of the family Bignoniaceae] bearing a capsule with 3 valves, the generic character is bivalve," and "Asters and *Solidagos* with the ligules mixt (sic) with the florets." Rafinesque could not tolerate genera in which there was variation in numbers of floral organs; therefore, he could easily imagine how a species might vary and become permanent for an abnormal number of petals, stamens, carpels, etc. To him, this would constitute the origin of a new genus. If the stabilized deviations were less significant, "such as mere color of flowers, size of stem, leaves, etc." (Rafinesque, 1836, p. 16), this would produce a new species. By operating from this taxonomic philosophy, he had no difficulty in naming the 2,700 new genera ascribed to him by Merrill (1949).

Returning to Rafinesque's ideas on evolution, there is set forth in the second paragraph (figure 2) a concept of "primitive species." These are the smaller number of ancestral species which, by the processes of mutation and stabilization, gave rise to the much larger number of present-day (he uses the word "actual") species. If evolution as we now conceive it involves a change through time, from ancestors to descendants, then Rafinesque is here expressing a very similar idea — a genealogy or family tree of living organisms. To paraphrase his views, we might say that all present species of monkeys evolved from one original "primitive species" of monkey; all dogs from one original species of dog; all roses from an original rose; all wheat from an original wheat, etc., *ad infinitum*. The way evolution really works goes deeper than Rafinesque could have possibly imagined. Ancestral wheat evolved from an earlier-existing grass, grasses from some earlier-existing monocotyledon, monocotyledons from some earlier-existing angiosperm, angiosperms from some earlier-

existing gymnosperm, and so on, back to the very beginnings of life on earth.

Rafinesque's concept of earth's history was limited by the geological knowledge of his day. Cuvier (1815), among others, was a powerful proponent of the theory of "catastrophism" as an explanation of geologic history as revealed in rocks. "Catastrophism, so far as its biological aspect is concerned, is essentially a device to preserve the leading tenets of Christian theology and at the same time to give these doctrines a scientific cast" (Eiseley, 1958, p. 67). Multiple series of catastrophic upheavals were assumed, the latest of which was the Noarchian Flood of the Bible. Prehistoric life had been successively exterminated, then recreated; or if the catastrophies were not world-wide, then survivors had migrated into the devastated regions to start life anew. Non-catastrophic theories to explain geological history had also been put forward (Hutton, 1795), but these were mainly rejected as being incompatible with dominant religious beliefs of the time. Rafinesque appears not to have been bound by a particular dominant geological theory (1833, pp. 191-193), but he did agree that successive water-deposited strata had exterminated earlier (fossil) forms of life. We may assume, therefore, that in his evolutionary theory, all the single "primitive species" of monkey, dog, rose, wheat, etc. were the survivors of — or were created after — the most recent catastrophic world-flood.

Finally, I would call attention to those parts of Rafinesque's musings that best demonstrate his qualities as a true scientist. In paragraph two, he states: "It is not impossible to ascertain the primitive Sp. that have produced all the actual; many means exist to ascertain it: history, locality, abundance, etc." His final paragraph speaks about a proposed research effort which could produce "a reduction of our flora from 8,000 to 1,200 or 1,500 primitive Sp. with genealogical tables of the gradual deviations having formed our actual Sp." In these brief sentences, he sets out a clear-cut plan of research, including methods (comparative morphology, biogeography, demographics) and goals (to chart the genealogy — hence, evolution — of some 8,000 American plant species). If only Rafinesque could have put aside all distractions and concentrated his intellect on this one subject long enough to write a definitive treatise on it, what a great impact that might have had on the biology of his day! Consider the fact that it took Darwin 20 years of concerted effort just to produce his 1859 book, which he viewed as only an "abstract" of a larger encyclopedic study on evolution.

Peattie (1936) may have been right that Darwin's timing and "publicity" made the difference in his success. Rafinesque's ideas, even if he had fully elaborated upon them, might have come too early and hence lacked impact. The history of science is not one of ideas alone, as though these had some ethereal existence apart from the all-too-human individuals whose intellectual powers we propose to honor. Ideas do complete, surely, but what interests us more are the people whose minds have created science's view of life and the universe. Rafinesque remains an enigma, but we understand him a little better, as a person and scientist, from this analysis of a few words he put on paper nearly 160 years ago.

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Differentiating *Mimulus jepsonii* and *M. nanus* in South-Central Oregon: A Problem in Applied Systematics¹

By Robert J. Meinke

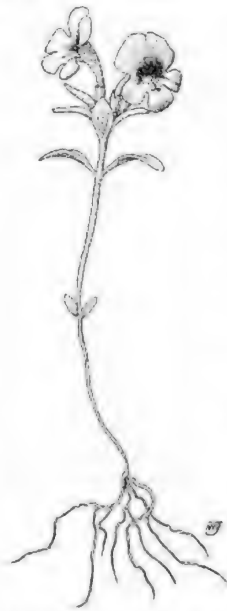
One of plant taxonomy's numerous goals is to provide a serviceable classification that biologists, foresters and other professionals can use to identify accurately species in the course of their work. Most workers rely exclusively on state or regional floristic manuals, such as **Flora of the Pacific Northwest** (Hitchcock and Cronquist 1973), which summarize the species for a given area based on the opinions of numerous taxonomic authorities. Although these extensive references are invaluable, size limitations often make it impossible to include adequately all the natural variation encountered during botanical field studies. This is particularly true if the focus involves rare or unusual taxa.

Mimulus jepsonii (Scrophulariaceae), a delicate, annual monkeyflower with purplish-red corollas, provides an example of the problems that can arise in distinguishing rare from more common species. First described by Grant (1924), the species belongs to the *Eunanus* section of the genus, characterized by low-growing annuals with yellow or reddish flowers, often occurring in dry, sandy sites. Peck (1961) reported that *M. jepsonii* occurred only from southern Klamath County (Oregon) to Nevada and California, with the majority of collections from northern California. Because of its apparent rarity, Siddall et al. (1979) recognized *M. jepsonii* as a potentially endangered species for Oregon. Later, it was placed on the Sensitive Species List maintained by Region 6 of the US Forest Service.

With inclusion on the Forest Service Sensitive Species List, *M. jepsonii* became, in effect, a protected plant on national forest lands in Oregon. Despite this status, little was known about the species outside of the limited information available in the floras (Munz 1959, Peck 1961), and a very outdated taxonomic monograph (Grant 1924). This lack of knowledge eventually became an acute problem, when abundant populations of red-flowered *Mimulus* were found on lands scheduled for timber harvest along the east flank of the southern Cascades Range. Botanists working in the four affected national forests, the Deschutes, Winema, Umpqua and Fremont, began having doubts concerning identification of these populations, despite careful use of available taxonomic keys. Many populations had members with at least some characteristics of *M. jepsonii*. However, many, and perhaps most, also showed a strong affinity to *M. nanus*, another member of the *Eunanus* group that is common and widely distributed east of the Cascades.

Although the morphological split between the two species seemed reasonable on paper (Grant 1924, Munz 1959, Peck 1961), applying the written descriptions and keys to plants in the field proved problematic. Habitat difference could not be used as a means to separate the species either, because virtually no ecological information was available.

Although Peck (1961) implied that *M. jepsonii* did not occur north of southern Klamath County, the Forest Service encountered populations of what seemed to be this taxon as far north as Deschutes County in central Oregon. University taxonomists confirmed this tentative identification, at least for the few collections submitted for determination. However, there were conflicting opinions concerning some specimens, and the identity of most populations remained unsubstantiated. Moreover, additional sites of *M. jepsonii*-like plants were being reported routinely, some of these mixed within populations of what were clearly *M. nanus*.



Mimulus jepsonii × 1

This investigation attempts to clarify the confusion associated with distinguishing *M. jepsonii* and *M. nanus* in Oregon. The Forest Service needed to know if the two species were distinct and if they could be readily separated in the field. It also needed to be determined whether the taxa actually co-existed in nature, or if this was a misperception based on morphological variation within species. By determining which, if any, of the populations were *M. jepsonii*, an informed decision could be made concerning the need for specific site protection and the overall status of the species in Oregon.

TAXONOMIC METHODS

Study Options

Various techniques can help decide if a group of similar populations or specimens represent one or more taxonomic entities. When questions are raised concerning species identification, the first step is to have a specialist evaluate available collections, under the assumption that simple misinterpretations of existing keys and descriptions may be the basis of the problem. If the puzzle persists, an integrated approach may be more productive. For example, it could be important to characterize habitat differences among sites and relate these to plant morphology. Perhaps plants that correspond most to descriptions of *M. jepsonii* associate

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with certain vegetation types or soil conditions. Life history traits could also be important. In other *Mimulus* groups, closely related species differ significantly with respect to breeding systems and germination requirements (Meinke 1983, 1992; Ritland and Ritland 1989). Field or greenhouse studies might reveal comparable distinctions in pollination or seed biology between *M. jepsonii* and *M. nanus*.

Herbarium studies might be augmented with cytological investigations, where potential difference in chromosome structure or number could be evaluated. However, chromosomes in *Mimulus* are very small and difficult to compare structurally. Perhaps the most definitive means to evaluate suspected species differences is via molecular studies, using a laboratory technique called *electrophoresis*. Electrophoretic studies of selected enzyme systems, using tissue samples from living plants, could detect biochemical divergence among populations and species. One could even search for chloroplast DNA mutations, a procedure commonly used today in the reconstruction of evolutionary histories and relationships of plants. However, there is no guarantee that chromosome studies or molecular biology would contribute to a practical classification for field use, even if genetic differences among populations were detected. This is because these types of variations, so important from an evolutionary perspective, are seldom correlated with external morphology at the species level.

A Focus on Morphology

After considering the alternatives, it was determined that an ecological survey combined with a morphological study, using a method known as Principal Component Analysis (PCA), would likely provide the most pragmatic approach to the *M. jepsonii* - *M. nanus* problem. This type of morphological evaluation is often called a *phenetic analysis*. In using PCA, an investigator selects x morphological attributes, then measures them on one or more plants from y populations. Usually 15-20 traits are measured at a minimum, and typically include floral as well as vegetative features. The investigator selects a range of characters for evaluation, usually including those considered important in the taxonomy of the study group, as identified by previous workers. PCA is useful in species separation studies, because it avoids the need for preconceived assumptions about which populations are thought to represent which taxa. Statistically, the procedure reduces the number of variables in the overall data set by forming linear combinations that explain most of the variability. In general terms, the analysis is designed to identify key morphologic features helpful in distinguishing the species, and will group populations as points on a graph, according to their overall similarity. For *M. jepsonii*-*M. nanus* sites in central Oregon, 20 traits (Table 1) were measured for 65 populations. These occurred from Deschutes to Klamath Counties, and were all sampled in 1991. Five plants were measured per site, and used to calculate a population average for each of the traits in Table 1. Included in the analysis, as a benchmark, was the type collection of *M. jepsonii* from California (Grant 1924). Type collections are important in taxonomy, because they

are the specimens upon which the original published description of a species is based. Finally, three living populations of *M. nanus* from Harney County, where *M. jepsonii* was not present, were added for comparison. The PCA program in the software package STATGRAPHICS was employed in the phenetic analyses.

Table 1. List of morphological traits measured from *Mimulus* plants for use in Principal Component Analysis (see discussion in text). Sixty-nine study populations were sampled. An average measurement was derived for each trait (from five samples per population) for use in the analyses.

- (1) Length of the longest root. (2) Combined length of first two internodes above cotyledons. (3) Length of initial stem leaf. (4) Width of initial stem leaf. (5) Length of upper cauline leaf. (6) Width of upper cauline leaf. (7) Peduncle length (in fruit). (8) Calyx length (in flower). (9) Calyx width (in flower). (10) Calyx length (in fruit). (11) Calyx width (in fruit). (12) Overall corolla length. (13) Corolla limb length. (14) Corolla limb width. (15) Corolla tube length. (16) Corolla tube width. (17) Distribution of hairs on the front of the corolla (on one, or both, corolla lips). (18) Length of upper corolla lip. (19) Width of upper corolla lip. (20) Length of capsule.

Forest Service botanists were concerned that phenology or microhabitat might determine morphology, and that plants identified as *M. jepsonii* might merely be growth forms of *M. nanus* influenced by environment. To address this problem, two separate PCA's were run. The first analysis utilized data measured in the field, using adult, flowering plants selected from each study population in mid to late June. The type collection of *M. jepsonii* (discussed above) was evaluated with this group. The second PCA used equivalent data, but these were recorded from greenhouse-cultivated individuals in late June. The greenhouse plants were raised together at Oregon State University, where they were grown from seedling transplants gathered several weeks earlier from 27 of the original 68 study sites. Transplants were used rather than germination from seed, because of the reported difficulty in getting these species to germinate well in the lab or greenhouse (Ezell 1971). The idea was to determine if plants from a common environment (i.e., the greenhouse) would be more homogeneous than plants from various field locations, presumably more subject to environmentally-induced variation. A trend toward homogeneity in the greenhouse would support the notion that only a single, variable species (presumably *M. nanus*) was represented in the populations selected for study.

Ecological observations of populations were recorded to complement the morphological evaluations described above. General inspections of vegetation and soil were made at each site to check for potential correlations with population differences recognized by morphological analysis. In addition, the pollination biology of selected populations was compared. Insect pollinators were recorded, and seed set measured in the field and greenhouse

(where pollinators were excluded). Seeds were gathered from populations in each national forest for two germination tests; i.e., (1) a pretreatment of cold storage at 3°C for two months prior to soaking; and (2) soaking 1-2 days after collection, without a cold treatment.

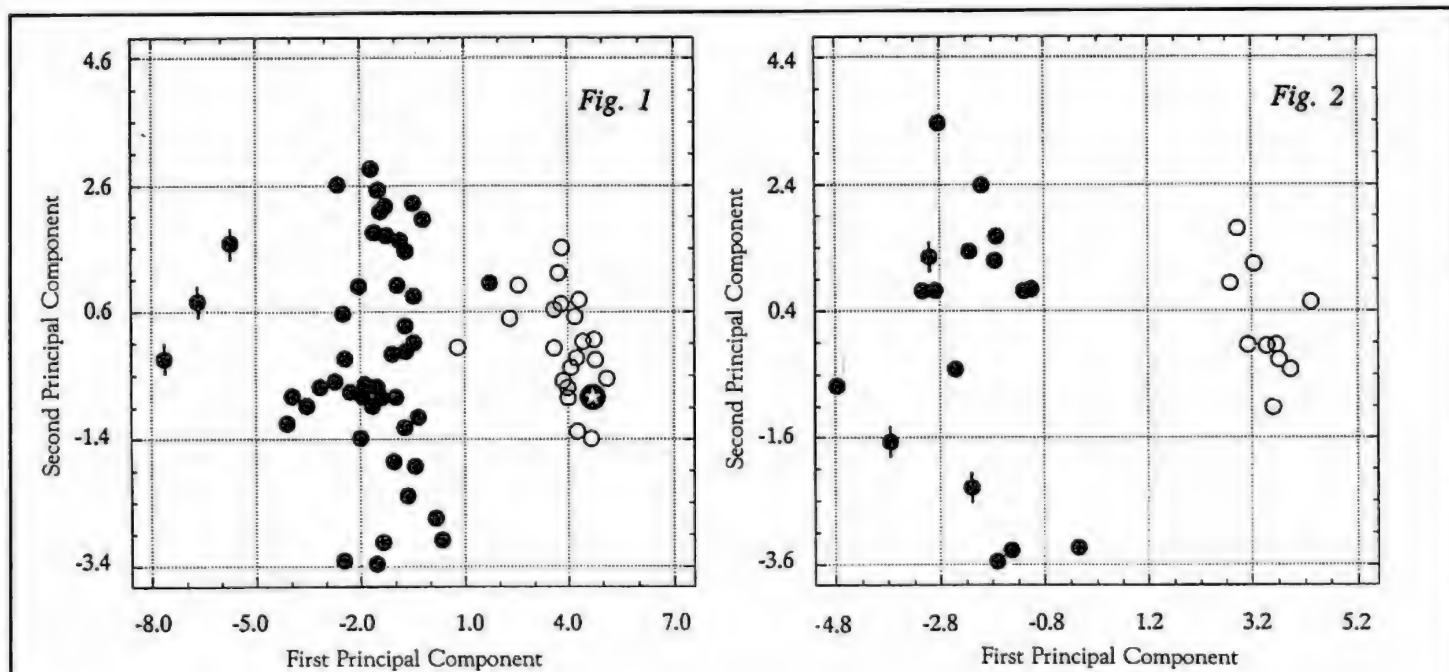
RESULTS

Morphological Differences

The PCA diagram (Figs. 1 and 2) clearly indicated that discrete taxonomic entities were present among the sampled populations, based on the traits used in the analyses. The open circles depict populations that generally match published descriptions of *M. jepsonii*. This determination was supported by the close association of these populations with the type collection of *M. jepsonii* (indicated by the star in Fig. 1). The dark circles represent populations that correspond to *M. nanus*, evidently the more variable of the two species, based on data point distribution. Comparison showed that growth in a common greenhouse environment (Fig. 2) did not result in convergence among populations, as might be expected if plants identified as *M. jepsonii* were solely the product of environmental modification. In fact, *M. jepsonii* appeared to become even more distinct when

grown together with *M. nanus*. It is also interesting that populations of *M. nanus* from the 65 main study sites near the Cascades appeared to be different morphologically from the populations from Harney County, indicated by the three circles on the far left of Fig. 1.

Several characteristics from Table 1 are apparently valuable in distinguishing *M. jepsonii* from *M. nanus*. Three of these; i.e., combined length of the first and second internodes, length of the longest root, and distribution of hairs on the front of the corolla, were identified by PCA as being particularly useful. In *M. jepsonii*, the initial internodes were usually considerably elongated in contrast to *M. nanus*, with flowers and upper leaves often appearing bunched toward the top. If they branched at all, *M. jepsonii* plants tended to do so well above the base, while *M. nanus* plants often branched near the base and became "bushy." In the greenhouse, *M. jepsonii* may branch out more than is typical in the field, but the internode character remains distinctive. The internode trait is not stressed in existing keys, and was first appreciated as diagnostic by David Thompson, a taxonomist in southern California who is interested in *Mimulus*. Roots are rarely of value in identifying differences among annual species, but these taxa are an exception. The intricate, finely branched roots of *M. nanus* ranged from 2-4 times longer than those of *M. jepsonii*, a tendency that re-



Figs. 1 and 2 (left to right). Results of Principal Component Analyses (PCA) of *Mimulus* populations.

PCA is a multivariate statistical technique that measures likeness among populations, based on selected aspects of plant morphology. (See text for discussion.) The traits used here are listed in Table 1. The symbols in the above diagrams indicate populations, with proximity a direct measure of morphological similarity.

Fig. 1 — PCA based on measurements taken from plants in the field. The dark circles represent *M. nanus* populations. The three circles on the far left (with vertical hatch marks) are from Harney County, while the 44 circles towards the middle depict the main study populations from central Oregon. Open circles represent *M. jepsonii*, with the star indicating the type collection.

Fig. 2 — PCA based on measurements taken from greenhouse plants grown from selected field populations. The symbols are the same as described for Fig. 1. Populations of *M. nanus* and *M. jepsonii* become less similar when grown in a homogeneous greenhouse environment, supporting their recognition as separate species.

mained evident even in the greenhouse. However, using this as a field character would require careful excavation. Finally, the differing arrangement of the corolla hairs on the front of the corolla was very specific — in *M. nanus* these were restricted to the extended, lower lip (sometimes called the lower “palate”), while in *M. jepsonii* they were plainly distributed above and below the opening of the corolla. They were whitish in color, and easy to spot with the naked eye, if flowers were fresh. This consistent trait was first recognized by Pennell (1951), but essentially ignored by others. Additional more or less diagnostic features of *M. jepsonii* include narrower leaves, and shorter calyces, corollas and capsules. Table 2 summarizes and quantifies important morphological differences between *M. jepsonii* and *M. nanus*.

Table 2. Summary of morphological differences observed between *Mimulus jepsonii* and *M. nanus* in central Oregon. Quantities represent averages \pm one standard error, with the range of the samples listed parenthetically. Five plants were measured per population.

Trait	<i>Mimulus jepsonii</i> (21 populations)	<i>Mimulus nanus</i> (47 populations)
Length of longest root (cm)	3.6 \pm 1.1 (0.8- 6.2)	8.9 \pm 3.6 (2.2-16.5)
Length of first two internodes (cm)	5.4 \pm 2.1 (1.7- 7.2)	1.8 \pm 0.8 (0.4- 5.6)
Length of longest stem leaf (cm)	1.6 \pm 0.5 (0.9- 2.7)	2.3 \pm 1.6 (1.4- 4.4)
Width of longest stem leaf (cm)	0.3 \pm 0.1 (0.1- 0.5)	0.9 \pm 0.6 (0.4- 1.5)
Length of flowering calyx (mm)	4.3 \pm 0.8 (3.4- 5.6)	7.1 \pm 1.4 (4.6- 8.8)
Width of flowering calyx (mm)	1.5 \pm 0.4 (1.1- 2.1)	2.2 \pm 0.9 (1.3- 3.3)
Length of fruiting calyx (mm)	5.3 \pm 1.0 (3.9- 6.9)	8.5 \pm 1.9 (5.9-10.0)
Width of fruiting calyx (mm)	2.2 \pm 0.6 (1.4- 3.1)	3.5 \pm 1.1 (1.9- 4.1)
Corolla length (mm)	10.2 \pm 1.6 (8.0-13.0)	18.1 \pm 5.0 (9.1-28.0)
Capsule length (mm)	5.3 \pm 0.9 (4.0- 7.1)	7.3 \pm 1.3 (5.0- 9.0)

Problems with Previous Descriptions

Characters determined by this study to be taxonomically useful were often disregarded in earlier keys, and therein lies much of the problem in appreciating the validity of *M. jepsonii*. Grant (1924) separated the two species by maintaining that the fruiting calyx of *M. nanus* became “distinct-

ly inflated” while that of *M. jepsonii* was “little or not at all inflated.” By comparing width/length ratios for both species, from Table 2, we can see that relative calyx dimensions did not change much from flower to fruit (0.35 \rightarrow 0.41 for *M. jepsonii*; 0.33 \rightarrow 0.41 for *M. nanus*). In any case, calyces of *M. nanus* did not become any broader than those of *M. jepsonii*. In Peck (1961), division between the species was also depicted as absolute. In *M. jepsonii* the corolla was listed as 1 cm. long, while in *M. nanus* it was stated to range from 1.5-2.0 cm. Table 2 shows that corolla length for both species deviated considerably from the range limits imposed by Peck (1961), who also set *M. jepsonii* apart by stating that its leaves were chiefly basal. This feature was virtually never noted among the several thousand *M. jepsonii* plants examined during the study, which generally bore most leaves several cm above the base! Munz (1959) likewise relied on corolla dimensions to separate the two species, allowing for a bit more leeway than Peck (1961) but still not conceding any overlap (9-11 mm vs. 13-20 mm). He also used calyx length as a key character, a feature that worked reasonably well but which, as with the corollas, was subject to enough variation to make it unreliable (Table 2). Holmgren (1984) added a recent twist, indicating that corolla length in *M. nanus* ranged from 1.0-1.5 cm, in complete contrast to Peck’s measurements.

Habitat Considerations

The populations identified as *M. jepsonii* usually occurred in small forest gaps, primarily with vegetation predominated by lodgepole pine (*Pinus contorta*), or occasionally ponderosa pine (*P. ponderosa*). *Mimulus nanus* is associated with the same two dominant tree species, but with the habitat preference reversed from that of *M. jepsonii*. Unfortunately, there is enough inconsistency in the distribution of the two species within these forest types to make plant community an unreliable indicator in species identification. *Mimulus nanus* also grows in a variety of scrub and steppe communities, although more commonly to the east of the study area.

A comparison of soil characteristics proved more valuable. Forest Service botanists reported many populations of *M. jepsonii* growing in so-called “popcorn” soil, a reference to the loose, very coarse sand or cobbles that resulted from depositions of pumice and volcanic gravels. In every case, populations identified by the PCA as *M. nanus* grew in this substrate. All populations designated as *M. jepsonii* grew in a heavier soil, containing some pumice but predominantly composed of finer particles that adhere when moist. The difference between the two soils was dramatically illustrated when seedlings and juveniles were transplanted to containers for transport to the greenhouse. The soil around *M. nanus* plants ran between fingers when scooped from the ground, often resulting in the untimely demise of transplants that were unable to tolerate bare roots. It seemed that in the study area, at least, the more substantial root systems of *M. nanus* may be an adaptation providing stability and enhanced moisture uptake in loose, dry soil. Conversely, the substrate supporting *M. jepsonii* populations could literally be sliced with a knife, and entire blocks could

be lifted out intact, much as one might cut a pan of brownies.

Reproductive Ecology

No significant differences for any aspect of reproduction were observed between *M. jepsonii* and *M. nanus*. On sunny days, populations of *M. jepsonii* and *M. nanus* were freely visited by various potential pollinators. Most common were solitary bees (families *Halictidae* and *Megachilidae*), long-tongued bees (family *Bombyliidae*), and several syrphid flies (family *Syrphidae*). The size and behavior of these insects suggested they were capable of pollinating *Mimulus* flowers of both species. Self-pollination is also possible for both species, but is generally inefficient. In the pollinator-free greenhouse, self-pollinating *M. jepsonii* flowers set an average of 13 ± 10 seeds per fruit (out of roughly 300-400 ovules!), while *M. nanus* flowers produced 18 ± 12 seeds in each capsule (both $N=15$). In the field, open-pollinated *M. jepsonii* flowers averaged 146 ± 43 seeds per capsule, and *M. nanus* flowers produced a mean of 225 ± 78 (both $N=15$). Germination for both taxa occurred only after seeds were subjected to cold temperature (3°C) prior to soaking, confirming the earlier report by Ezell (1971). Out of 300 seeds per species, 45 germinated for *M. nanus* and 78 for *M. jepsonii*. These low percentages might be enhanced by providing a longer pretreatment, or by soaking seeds during refrigeration. (They were merely kept damp in this instance.)

DISCUSSION

General Conclusions

Most of us have been frustrated by plants that, despite our best effort, cannot be satisfactorily keyed out. Such was the case here, where Forest Service botanists and others encountered local variations in *Mimulus* unaccounted for in available manuals and floras. A statistical evaluation of samples from four national forests confirmed that two monkeyflower species were indeed present. There was remarkably little overlap between the species at the population level, despite the fact that individual specimens did not always conform to the criteria in the existing manuals. Twenty-one *M. jepsonii* populations were identified in this study. All were confined to the Deschutes and Umpqua National Forests and were distributed along the east slope of the Cascades, from central Deschutes County south to Diamond Lake. The south shore picnic area at Diamond Lake was the best place to see showy displays of *M. jepsonii*, which peaked in late June and early July in 1991. This site had fair to good precipitation in March.

Two factors contributed to the difficulty workers had in identifying *M. jepsonii*. First, Forest Service botanists are typically restricted to a limited area of operation, often focusing on a single ranger district or timber sale. Consequently, there was little opportunity to evaluate *Mimulus* populations over a wide enough range to pick up the differences among forests. Second, a great deal of phenotypic

plasticity (i.e., variation in plant appearance) occurred within most *M. nanus* populations, increasing the potential for misidentification. This is a common phenomenon for many of our widespread monkeyflowers (Hiesey et al. 1971, Vickery 1978). In large plant populations, especially in cross-pollinating annuals such as *Mimulus*, morphological oddities commonly result from environmental factors or novel genetic expression. Those who have botanized in central Oregon know that *M. nanus* populations can be immense in favorable years. As a result, it is not unexpected to find occasional plants that more or less correspond to published descriptions of other species, particularly *M. jepsonii*. These individuals develop smaller than normal flowers, and may also produce elongate internodes and unusually narrow leaves. Early in the study, it was suspected that some of the Forest Service reports of *M. jepsonii*, principally from Lake and Klamath Counties, probably represented aberrant individuals of *M. nanus* scattered among thousands of "normal" plants. Field work conducted during the study supported this impression. As previously stated, *M. jepsonii* and *M. nanus* were never seen to occur together, a condition possibly due to different substrate preferences.

Identification

To separate *M. jepsonii* from *M. nanus*, first evaluate distribution of corolla pubescence. The presence of scattered hairs on the lower and upper lips always denotes *M. jepsonii*. The remaining characters summarized in Table 2, and the key below, confirm the identification, particularly if corollas are shriveled or absent. As additional evidence, the investigator should take note of the habitat, specifically soil characteristics.

Whenever doubt persists, plant morphology throughout the population should be surveyed before settling on species determination. Examination of a number of individuals in a population should help determine whether a particular variation is consistently represented, or merely a quirk. Intraspecific variability is frequently the basis for problems encountered in keying out plants.

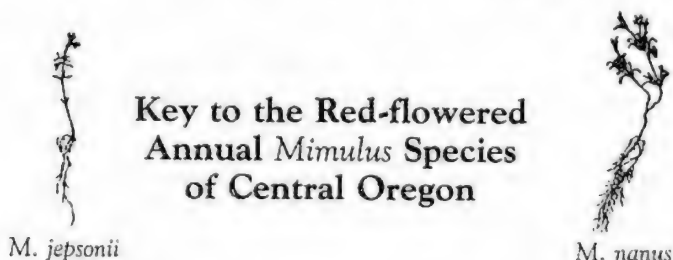
Further Questions

Is the morphological diversity reported here for *M. jepsonii* and *M. nanus* representative of the two species throughout their ranges? Perhaps not, at least as far as *M. nanus* is concerned. It is evident that populations of this species from Harney County were most similar to each other (Fig. 1), implying that *M. nanus* may consist of distinct geographic races. Regional variation in the species was also observed by Ezell (1971), who suggested in his doctoral dissertation that certain Cascadian *M. nanus* populations should be recognized as a distinct subspecies i.e., subsp. "*cascadensis*". Ezell (1971) also proposed that *M. jepsonii* be reduced to a subspecies of *M. nanus*. One could argue that Fig. 1 supports this position, because *M. jepsonii* appears to be no more unique than the outlying populations of *M. nanus* from Harney County. However, when *M.*

nanus was grown in the greenhouse, the Harney County plants lost much of this distinction (Fig. 2), suggesting that any "racial" separation between eastern and central Oregon plants is overcome by a common growth environment. *Mimulus jepsonii*, on the other hand, did not lose its identity.

Should *M. jepsonii* be maintained as a distinct species? The answer is an unequivocal "yes," based on what we have learned here. Clearly, it is a separate entity from *M. nanus*, and the morphological relationship between the two taxa is more distant than is traditionally attributed to subspecies or varieties. Of course, it is possible that differences between the species break down outside of Oregon. However, the fact that the type collection of *M. jepsonii* (from the Mt. Lassen area in California) clustered so well with the Oregon populations (in Fig. 1) implies the contrary. Moreover, the separate identities of the species have apparently not come into question in California, although this may be due to their geographic and elevational ranges being more dissimilar farther south.

How should the information gained here influence management of *M. jepsonii*? We now know that in Oregon, at least, the species is less widespread than reported earlier. Nonetheless, *M. jepsonii* is not exactly uncommon, and in some areas it can be locally abundant, particularly where moderate forest disturbance has occurred. As of now, however, there is no firm evidence that the species benefits from disturbance, and further studies are in order. *Mimulus jepsonii* occurs at the northern edge of its range in our area, and it will surely benefit the genetic diversity of the species if Oregon populations are preserved. Besides, Jepson's monkeyflower provides one of the few splashes of springtime color in an otherwise drab lodgepole pine understory, and perhaps that is justification enough for keeping it around.



Key to the Red-flowered Annual *Mimulus* Species of Central Oregon

- 1 Pedicels from 3-12 mm long, nearly equalling or exceeding the calyx; corollas up to about 7 mm long; moist microsites in or near the mountains *M. breweri*
- 1' Pedicels less than 4 mm, always much shorter than the calyx; corollas usually longer than 8 mm; plants widespread, often in low, arid habitats.
- 2 Corolla 8-10 (-12) mm long, with hairs above and below the corolla orifice; leaves nearly linear to \pm oblanceolate; first 2 internodes elongate, up to 7 cm long, plants usually branched well above the base; from near the Cascade Mountains, usually in mesic lodgepole forest, rarely in dry, sandy soil *M. jepsonii*
- 2' Corolla (9-) 12-35 mm long, with hairs limited to the lower palate (lip); leaves oblanceolate to ovate; first internodes not usually much elongated; in a variety of mostly xeric sites, typically in loose, sandy soil.

- 3 Major stem leaves (10-) 14-30 mm wide, broadly ovate, acute; flowering calyx 8-15 mm; herbage with a mephitic (skunky) odor *M. cusickii*
- 3' Major stem leaves 4-14 mm wide, oblanceolate, mostly obtuse; flowering calyx 4-9 mm; herbage odorless *M. nanus*

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Some Recent Taxonomic Changes Affecting the Names of Oregon Plant Species

By Kenton L. Chambers


Books, like people, grow old and eventually need to be retired. The principal floristic manuals covering the flora of Oregon are reaching this venerable state. These include **Manual of the Higher Plants of Oregon** (Peck, 1961), **Illustrated Flora of the Pacific States** (Abrams, 1923, 1944, 1951, 1960), **A California Flora** (Munz and Keck, 1959), **Vascular Plants of the Pacific Northwest** (Hitchcock and Cronquist, 1973). Such works are still extremely useful, their detailed keys, descriptions and illustrations allowing identification and naming of virtually all native and introduced species of the state. As newer books are published, however, like the forthcoming revised version of **Manual of the Flowering Plants of California** (Jepson, 1925), older reference manuals will gradually lose their utility and scientific rigor. They will not represent current knowledge about species names and relationships based on the best and most recent taxonomic research.

The pace of new research in systematics (plant taxonomy, in the broad sense) continues at a high rate in botanical institutions all over the world. Studies by taxonomists in countries as far away as Europe and the Orient have to be examined for new insights about the relationships and classification of Oregon's flora. Botanists who wish to keep abreast of taxonomic research have at least two difficult problems to overcome; first, they must be aware of pertinent publications throughout the vast scientific literature, and second, they must check and evaluate taxonomic conclusions derived from such research. The most critical publications to Oregon botanists are those which propose significant changes in names and classification of particular Oregon genera. Botanists are almost never forced to adopt new names for familiar plant species; changes are usually optional, based on evaluation of the quality of supporting research and reasonableness of the authors' conclusions. Only if existing plant names are found to be unusable (e.g., "illegitimate") because of particular rules in the International Code of Botanical Nomenclature (ICBN) are we literally forced to abandon them.

The purpose of this article is to list and comment on some proposed changes in the names of Oregon plant species. These changes are the result of recently published tax-

onomic research. Biologists constantly deal with plant names; however, once we have memorized Latin names for numerous species, it is disconcerting, to say the least, to find other botanists using different names. We ask ourselves, "What goes on here; what's the excuse for changing names?" Perhaps it is a simple difference, such as a letter or two in the spelling of a name. For example, both *Sidalcea malvaeflora* and *Polygonum phytolaccaefolium* bear misspelled species names. Correct are *malviflora* and *phytolaccifolia*, as mandated by a provision in ICBN permitting only the letter "i" as a connecting vowel in compound words of Latin origin. The connector "ae" is not allowed, even though 19th century botanists who originally named these species used it. Likewise, *Pachistima* (Celastraceae) must be spelled *Paxistima* (Chambers, 1992), because the latter name was legitimately published, while the former was not. Other recent changes that we have selected, below, are more significant, representing major differences from the reference manuals listed earlier. No doubt many of the changes will be adopted in the upcoming revised edition of Jepson's manual, as well.

Research leading to rearranging generic relationships is a frequent source of new and unfamiliar plant names. The category of genus is basic and indispensable to nomenclature. By merely speaking the name of a genus (*Rhododendron*, for example), we call to mind a constellation of diagnostic traits — a mental picture, so to speak — by which we recognize a large group of related species. A change in the name of a genus is indeed a major event, which may alter our views of species relationships. Modern systematics research is exposing many past errors in classification, however, and the advance of science cannot be held back simply by nostalgia for familiar plant names.



A good example of correcting past taxonomic errors is the recently-published research by Chuang and Heckard (1991) on the genera *Castilleja* and *Orthocarpus* (Paintbrush and Owl-clover, Scrophulariaceae) and their relatives. The traditional genus *Orthocarpus* is shown to be an artificial assemblage of three evolutionary lines; one line properly belongs within *Castilleja*, another retains the name *Orthocarpus*, and the

third stands as an independent genus named *Triphysaria*. Impressive evidence from chromosome numbers, pistil and ovule morphology and corolla structure supports the authors' conclusions. Species of Oregon that must change their names are as follows (current name at left, new name at right):

Orthocarpus attenuatus = *Castilleja attenuata* (Gray)
Chuang & Heckard

Orthocarpus campestris = *Castilleja campestris* (Benth.)
Chuang & Heckard

Orthocarpus castillejoides = *Castilleja ambigua* Hook.
& Arn.

Orthocarpus erianthus = *Triphysaria eriantha* (Benth.)
Chuang & Heckard

Orthocarpus faucibarbat = *Triphysaria versicolor*
Fisch. & Mey. subsp. *faucibarbat* (Gray) Chuang &
Heckard

Orthocarpus hispidus = *Castilleja tenuis* (Heller)
Chuang & Heckard

Orthocarpus lacerus = *Castilleja lacera* (Benth.)
Chuang & Heckard

Orthocarpus lithospermoides = *Castilleja rubicundula*
(Jeps.) Chuang & Heckard subsp. *Lithospermoides*
(Benth.) Chuang & Heckard

Orthocarpus pusillus = *Triphysaria pusilla* (Benth.)
Chuang & Heckard



Taxonomic studies of the Portulacaceae being completed at Oregon State University support earlier proposals by Swanson (1966) and McNeill (1975) that several species of *Montia* should be returned to *Claytonia* (Springbeauty), where they in fact resided 100 years ago. This brings into *Claytonia* some annual species as well as perennials with slender taproots or rhizomes. They join presently accepted *Calytonia* species whose perennial roots are tuber-like or thick and elongated. All species of the reconstituted genus *Claytonia* have their principle leaves in a basal rosette, the flowering stems naked except for a distinct pair of opposite, sometimes fused leaves (bracts) just below the cyme of flowers. Species of Oregon *Montia* whose names are to be changed are as follows:

Montia arenicola = *Claytonia arenicola* Hend.

Montia cordifolia = *Claytonia cordifolia* Wats.

Montia heterophylla (of Peck's Manual) = slender-leaved races of *Claytonia sibirica*

Montia perfoliata divides into three species, *Claytonia perfoliata* Willd., *Claytonia rubra* (Howell) Tidest., and *Claytonia parviflora* Hook. (not the same as *Montia parvifolia*!).

Montia sibirica = *Claytonia sibirica* L.

Montia spathulata = *Claytonia exigua* Torr. & Gray



Another recent change which involves resurrecting a long-ago accepted name for a well-known species is the transfer of *Sisyrinchium douglasii* (Grass-widows, Iridaceae) to the genus *Olsynium* (Goldblatt, et al., 1990) Not since early in this century (Piper, 1906; Abrams, 1923) has the latter name been used in floras for the Pacific Northwest. As Oregon botanists know, "*Sisyrinchium*" *douglasii* (now known as *Olsynium douglasii* [A. Dietr.] Bickn.) differs sharply from the blue- or yellow-flowered *Sisyrinchium* species of the state in having a reddish-purple (rarely white) perianth (often called petals, but really tepals), only partly fused stamen filaments and round rather than angled stems. According to Goldblatt et al. (1990), these obvious differences are reinforced by more subtle traits of the leaf blade and sheath, roots and seeds, all linking *O. douglasii* to a dozen or more South American species which together comprise the genus *Olsynium*. The "species" *Sisyrinchium inflatum* (Hitchcock and Cronquist, 1973) has recently been renamed *Olsynium douglasii* var. *inflatum* (Suksd.) (Cholewa and Henderson, 1991). Interestingly, the work by Goldblatt et al. (1990) keeps Golden-eyed-grass (*Sisyrinchium californicum*) safely within *Sisyrinchium*, not segregating it into the genus *Hydastylus* as was done by Piper and Abrams (op. cit.).



Molecular systematic studies figured in another recent re-establishment of a former genus name, this time in the Asteraceae (Compositae). *Uropappus* (Silver-puffs) was merged with *Microseris* as long ago as 1866, but was kept separate by both Jepson (1925) and Peck (1961) to comprise the single species *U. linearifolius*. The species was placed in *Microseris* by Chambers in Abrams (1960) and by Cronquist in Hitchcock et al. (1955); the correct species epithet is *lindleyi* rather than *linearifolia*, however. Jansen et al. (1991) have revised the classification of *Microseris* and related genera, using the newly popular molecular technique of restriction enzymes to detect mutations in the DNA of chloroplast chromosomes. Ideally, such mutations are neutral to natural selection, arising and persisting essentially by chance. Therefore, over geologic time, an evolving plant group will accumulate increasing numbers of unique shared mutations. The term given to a set of shared advanced traits (in the case at hand, point mutations of the DNA) is "synapomorphies." Statistical tests of the data by Jansen et al. (1991) grouped typical species of *Microseris* 100% of the time by their molecular synapomorphies, but in 98% of the tests, *Lindleyi* was excluded from the genus. It was placed on its own separate evolutionary line, sharing significant synapomorphies with two other genera — *Agoseris* and *Nothocalais*. We know that *lindleyi* differs from typical *Microseris* in important morphological traits as well (e.g., pubescence, growth-form, involucre, fruit shape, pappus), but polyploid hybrids connect it with two *Microseris* species. By renaming it *Uropappus lindleyi* (DC.) Nutt., we emphasize its morphological, genetic, and evolutionary distinctness from *Microseris*. Furthermore, *Nothocalais* is defined as a natural generic group by the inclusion of

"*Microseris troximoides*," now *Nothocalais troximoides* (Gray) Greene, and "*Agoseris alpestris*," now *Nothocalais alpestris* (Gray) Chambers (Abrams, 1960).

Phylogenetic analysis of a different kind, relying on morphology and anatomy rather than chloroplast DNA, led Kron and Judd (1990) to very interesting conclusions about the status of the genus *Ledum* (Labrador-tea, Ericaceae). In a study of the large and diverse genus *Rhododendron*, relying on morphological synapomorphies as evidence for shared common ancestors within sections of the genus, they found that *Ledum* is evolutionarily connected with a particular *Rhododendron* species-group (section *Edgeworthia* of subgenus *Rhododendron*). Its phylogenetic origin is therefore deeply embedded within this latter genus, and it ought not stand on its own generically. In particular, it shares a unique type of shield-shaped epidermal trichome (multicellular hair) with this species-group. If we view *Ledum* as essentially an advanced, morphologically divergent *Rhododendron*, then logically the two genera should be merged. The Oregon taxon *Ledum glandulosum* takes the new name of *Rhododendron neoglandulosum* Harmaja (Wallace, 1992).



The reverse of generic "lumping" (as in *Ledum*) is "splitting;" i.e., the chopping-up of large, polymorphous genera into smaller, more homogeneous species-groups which are named as separate genera. An example of a worldwide, diverse genus in which this is taking place is

Polygonum (Knotweed, Smartweed, Bistort, etc., of Polygonaceae). These smaller groups, which we call segregate genera, have not yet become popular among American botanists, but the changing fashions of taxonomy may in the future bring *Polygonum* segregates like *Aconogonon*, *Bistorta*, *Fallopia*, *Persicaria* and *Reynoutria* into our floras and manuals (Weber, 1987). According to Hong (1991) there are two "*Polygonum*" species in Oregon which belong to *Aconogonon*; our reference manuals know these as *Polygonum phytolaccifolium* and *Polygonum newberryi*. If Oregon taxonomists in the future agree to split *Polygonum*, these would become *Aconogonon phytolaccifolium* (Small) Rydberg and *Aconogonon davisiae* (Gray) Sojak. Hong merged *newberryi* with *davisiae*, an alpine species of California and southwest Oregon; however, many other taxonomists, past and present, have kept these two species separate. It would be an interesting project for a taxonomy student to study these taxa by modern methods and tell us whether two species or only one ought to be recognized.



A generic split that was made in the Onagraceae by Raven (1969) involved segregating a large number of species of *Oenothera* into *Camissonia*. Raven's concepts have been widely accepted by taxonomists but have not yet found their way into regional floristic manuals. *Oenothera*, as delimited in its new, narrower sense, contains only those species having a deeply four-lobed stigma. It includes the beautiful cultivated Evening-primroses such as *O. glazioviana* Micheli (formerly known as *O. erythrosepala*), rare taxa like *O. villosa* Thunb. (formerly known as *O. strigosa*). *Camissonia*, on the other hand, is composed entirely of species having a capitate (pinhead-like) stigma. The

following list identifies the Oregon species of "*Oenothera*" affected by this change, together with their correct names (excluding subspecies) in *Camissonia*:

Oenothera alyssoides = merged with *Camissonia boothii*

Oenothera andina = *Camissonia andina* (Nutt.) Raven

Oenothera boothii = *Camissonia boothii* (Dougl.) Raven

Oenothera cheiranthifolia = *Camissonia cheiranthifolia* (Spreng.) Raimann

Oenothera claviformis = *Camissonia claviformis* (Torr. & Frem.) Raven

Oenothera contorta = *Camissonia contorta* (Dougl.) Kearney

Oenothera graciliflora = *Camissonia graciliflora* (Hook. & Arn.) Raven

Oenothera heterantha = *Camissonia subacaulis* (Pursh) Raven

Oenothera minor = *Camissonia minor* (A. Nels.) Raven

Oenothera ovata = *Camissonia ovata* (Torr. & Gray) Raven

Oenothera palmeri = *Camissonia palmeri* (S. Wats.) Raven

Oenothera pterosperma = *Camissonia pterosperma* (S. Wats.) Raven

Oenothera pygmaea = *Camissonia pygmaea* (Dougl.) Raven

Oenothera scapoidea = *Camissonia scapoidea* (Torr. & Gray) Raven

Oenothera tanacetifolia = *Camissonia tanacetifolia* (Torr. & Gray) Raven

Raven (1969) also noted two additional species occurring in eastern Oregon — *Camissonia parvula* (Torr. & Gray) Raven, and *Camissonia pusilla* Raven — but he excluded *Camissonia pubens* (S. Wats.) Raven (*Oenothera pubens*, cited in Hitchcock & Cronquist, 1973) from the state.

Another large genus of Onagraceae, reviewed in detail by Raven and coworkers, is *Epilobium* (Willow-herb, Fireweed). Several Oregon species have received new names based on this work. *Epilobium paniculatum*, for example, has to be called *E. brachycarpum* Presl, for reasons of nomenclatural priority. Closely related to *E. minutum* but distinct from it in chromosome number, seed morphology and growth habit is *E. foliosum* (Torr. & Gray) Suksd. (Seavey et al., 1977). This is an addition to the state's known flora, not listed before in standard reference books. In a third case, five names that have been applied to one of

our most abundant, often weedy epilobiums have been merged under a still older name. *Epilobium adenocaulon*, *E. californicum*, *E. franciscanum*, *E. glandulosum* and *E. watsonii* have all been reduced to synonyms of *E. ciliatum* Raf.



Finally, the beautiful and striking orange-red flowered species of California and southwestern Oregon known as *Zauschneria latifolia* (California Fuchsia), when carefully analyzed by Raven (1976), proved to be very closely related to *Epilobium*. The case is similar to that of *Ledum*, described above. *Zauschneria* evolved its large, red, tubular flowers through specialization for pollination by hummingbirds. Except for this feature, it is similar in chromosome number and vegetative morphology to *E. nivium*, a typical purple-flowered, bee-pollinated epilobium. To express this relationship and to show the evolutionary origin of *Zauschneria* from within *Epilobium*, Raven has renamed the California Fuchsia *E. canum* (Greene) Raven. Note that the species name *latifolium* had to be replaced, because there already exists a different species named *E. latifolium* L. (Red Willow-herb).



Important generic splitting in the Polemoniaceae done by Grant (1956) 36 years ago has been adopted in some, but not all, of the books on Oregon's flora. The large and biologically complex genus *Gilia* has been studied in detail by Grant and his coworkers since the early 1950's. *Gilia* contains several distinct species-groups and is itself closely related to other recognized genera such as *Eriastrum*, *Langloisia* and *Navarretia*. From his analysis of the genetic, morphological and cytological relationships within *Gilia*, Grant (1956) proposed separate generic status for two species-complexes, called *Allophyllum* and *Ipomopsis*, both of which are represented in Oregon. *Ipomopsis*, according to Grant, differs from typical *Gilia* in basic chromosome number, vegetative habit, seeds, corolla shape and breeding behavior. It is recognized as a genus by Munz and Keck (1959) but not by Peck (1961) nor Cronquist (Hitchcock et al., 1959; Cronquist et al., 1984) Species of *Ipomopsis* are assigned by Cronquist (1984) to two sections (sect. *Microgilia* and sect. *Ipomopsis*) of *Gilia*. The best known Oregon species to be affected by these differing taxonomic views is *Ipomopsis (Gilia) aggregata* (Pursh) V. Grant (Scarlet Gilia, Skyrocket). Much interesting research on pollination, hybridization and floral evolution has been published in recent years about this species and its relatives, which occur widely throughout western North America. Most of this literature is referenced by the names assigned to the taxa in *Ipomopsis*, rather than in *Gilia*. Besides this well-known showy species, other members of *Ipomopsis* in Oregon are: *I. congesta* (Hook.) V. Grant (*Gilia congesta*), *I. minutiflora* (Benth.) V. Grant (*G. minutiflora*), *I. polycladon* (Torr.) V. Grant (*G. polycladon*) and *I. tenuituba* (Rydb.) V. Grant (*G. aggregata* var. *macrosiphon*). The races of *I. aggregata* occurring in Washington, Oregon and northern California have mostly been classified as subsp. *formosissima* (Greene) Wherry. Also present in the Rogue River Valley, Oregon, is a member of Grant's other segregate genus *Allophyllum*, the rarely collected *Allophyllum gilioides* (Benth.) A. & V. Grant (*G. gilioides* in Peck's Manual).



The name of William C. Cusick (1842-1922) is well known among western American taxonomists, due to his pioneering work as a plant collector and contemporary of such "greats" of Oregon botany as Thomas J. Howell, Wilhelm Suksdorf and Lewis F. Henderson. Cusick has many plant species named in his honor, but the genus name *Cusickia* by M.E. Jones, published in 1908 for what we now call *Lomatium minus*, is no longer in use. Rollins (1988) remedied the need (if such existed) for an active generic name honoring Cusick. *Cusickiella* (Rollins, 1988) of Brassicaceae (Cruciferae) comprises two species which formerly were placed in *Draba*. One of these is widespread in eastern Oregon, *Cusickiella douglasii* (Gray) Rollins (*Draba douglasii*). This newly-described genus differs from *Draba* in having seeds with incumbent cotyledons; its seeds are larger and neither compressed nor grooved; and its 1- or 2-seeded fruits have more thickened, leathery valves and replum than are typical of *Draba*.



One of Oregon's and northern California's rare gentians has only recently been correctly described and named. *Gentiana plurisetosa* C.T. Mason (1990) from the Siskiyou Mountains was previously confused with *G. setosa* Gray, quite a different species. In an unusual mixup of names, *G. setosa* was found to be the same species as *G. bisetata* T. Howell of southwestern Oregon (Chambers and Greenleaf, 1989). The type specimen of *G. setigera*, from Mendocino County, California, had been wrongly interpreted by most California botanists, and this name was misapplied to *G. plurisetosa* (Jepson, 1925; Abrams, 1951; Munz and Keck, 1959). In Oregon, *G. plurisetosa* is known from montane meadows in the vicinity of Oregon Caves, whereas *G. setigera* is common in *Darlingtonia* bogs of the western Siskiyou of Josephine and Curry Counties.

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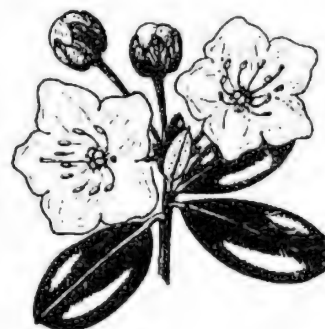
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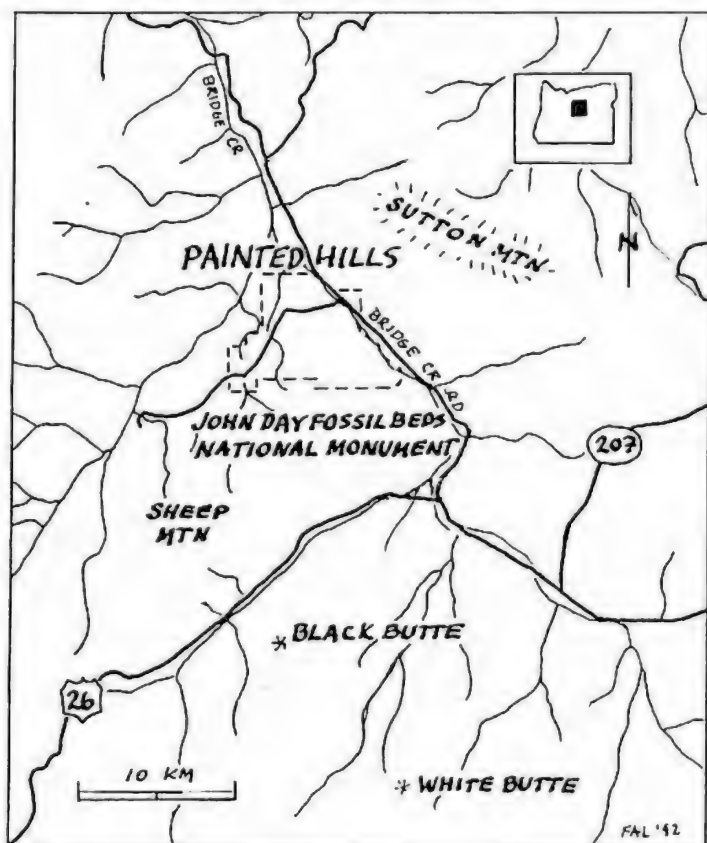
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OREGON PLANTS, OREGON PLACES¹

The Painted Hills: Thirty Million Years of Phytogeography

By Stuart Garrett and Berta Youtie

The Painted Hills Unit, John Day Fossil Beds National Monument lies at 600 meters (1970 ft.) above sea level about 15 km. (9 mi.) northwest of Mitchell, Oregon along Bridge Creek, a tributary of the John Day River.



This area is a spectacular combination of unusual geological features and varied plant life. The climate is semi-arid with most precipitation occurring during winter. It is hot and dry in summer.

The 5,668 hectare (14,000 acre) John Day Fossil Beds National Monument is administered by the Department of the Interior through the National Park Service. In 1947, the Howard and Avery families deeded 2.5 hectares (13 acres) at Painted Hills to the State of Oregon as a state park. This initial acreage was expanded and added to the National Monument when the National Park Service took over management in 1975.

The National Monument consists of the Painted Hills, Clarno and Sheep Rocks units. The 1,247-hectare (3,080 acre) Painted Hills unit is an excellent area in which to study the effects of climate, geological forces, and humans

on plant life. Fossils in local geological formations allow observations of more than 30 million years of earth's history.

Human History

Native Americans lived in John Day Valley for at least 8,000 years. The Painted Hills area divided Plateau and Great Basin (Paiute) cultures. Both groups made extensive use of plant resources in the area. The roots, nuts, seeds and berries of a variety of plants were used for food, medicine, shelter, cordage and ceremony. Biscuitroot (*Lomatium* spp.), also called wild celery or, in Indian terminology, "kouse," was an important staple of the Indian diet. Bitterroot (*Lewisia rediviva*) roots were peeled and boiled prior to eating. Camas (*Camassia quamash*) bulbs were dug as flowers faded and were baked in underground pits lined with balsamroot (*Balsamorhiza* spp.) leaves. Even the stems, fruits and roots of prickly-pear cactus (*Opuntia* sp.) were consumed. Fiber was obtained from willow (*Salix* sp.), Indian hemp (*Apocynum* sp.) and cattail (*Typha latifolia*). Bows were manufactured from juniper (*Juniperus occidentalis*) (Zucker et al. 1983).

Native Americans developed a pattern of seasonal travels which allowed them to visit particular sites for selected resources. Spring was a time for root digging and salmon harvest. Summer was used for travel to sites to take advantage of ripening fruits and seeds and for collection of fiber materials. Berry gathering and drying occurred in the fall. Winter saw reduced travel. Stored plant foods provided sustenance during this season of scarcity.

From a paleobotanical standpoint, Native Americans were the first people known to appreciate the plant fossils of John Day country. In the 1980's an archaeological research team from the Oregon Museum of Science and Industry found five small rock slabs with fossil leaf impressions in the corner of a house pit being excavated (Ashwill 1987).

The initial contact between Plateau culture Native Americans and Euro-Americans was with the Lewis and Clark expedition in 1805. The first Euro-Americans to extensively travel and explore the region were trappers. The Astorians, a group of fur trappers sent out by John Jacob Astor, followed in 1811. An unfortunate member of this party gave his name to the John Day River. John Day, a trapper from Virginia, became lost and was robbed by Native Americans near the mouth of the river that now bears his name (Brogan 1964).

¹ One of Oregon's great treasures is its biological diversity. "Oregon Plants, Oregon Places," a regular feature of *Kalmiopsis*, highlights Oregon's natural diversity. We will emphasize important geological, cultural and biological qualities of special Oregon places. Use these articles as guides to explore our remarkably diverse state.

In the summer of 1864 Captain John M. Drake of the US Army, stationed at Camp Maury on the upper Crooked River, noted that some of his cavalry had found fossil sea shells and mammal bones while pursuing "Snake Indians" (Paiutes). A minister named Thomas Condon accompanied soldiers to the area in 1865. Condon's interest in paleontology and geology eventually led to his appointment as the first Professor of Geology at the University of Oregon. Condon found fossils on Bridge Creek that would later make him and the area famous. He noted in a letter to geologist Dr. John Strong Newberry (Clark 1989), "On my last visit to the place of the outcrops I found some new things, new leaves, new fruit... as the region when I was there was infested with hostile Indians whose fresh tracks were on the trail I traveled, I could examine but little of the surroundings." Condon's correspondence with renowned paleontologists eventually catapulted the John Day Basin into international fossil fame.

The first settlers of the Painted Hills area were ranchers exploiting rich plant resources. Lowlands held stands of giant wild rye (*Elymus cinereus*). The uplands were rich with other native bunchgrasses. Large numbers of cattle and sheep were introduced to provide meat for gold miners in the Canyon City country to the east. Alterations of native plant communities began then and continued until the National Park Service fenced livestock from the Monument in 1980.

Geologic History

Bridge Creek Basin geologic formations are arranged like a layer cake. All strata located at, or visible from, Painted Hills are volcanically derived or are the result of erosional reworking and soil building of volcanic deposits. From the older (40 million years ago [mya]) and lower elevation Clarno Formation to the younger (15 mya) and higher elevation Columbia River basalt flows, these rocks form a remarkable geologic sequence that is internationally recognized for its contributions to paleontology and volcanic stratigraphy (Baldwin 1976).

Cenozoic Age of Mammals	Holocene	10,000 yrs. ago	
	Pleistocene	3 mil. yrs. ago	Landslides
	Pliocene	12 m.y.a.	Rattlesnake Formation
	Miocene	25 m.y.a.	Mascall Formation
	Oligocene	40 m.y.a.	Picture Gorge Basalt
	Eocene	60 m.y.a.	John Day Formation
Mesozoic Age of Reptiles			Clarno Formation
	Cretaceous	100 m.y.a.	Goose Rock Conglomerate

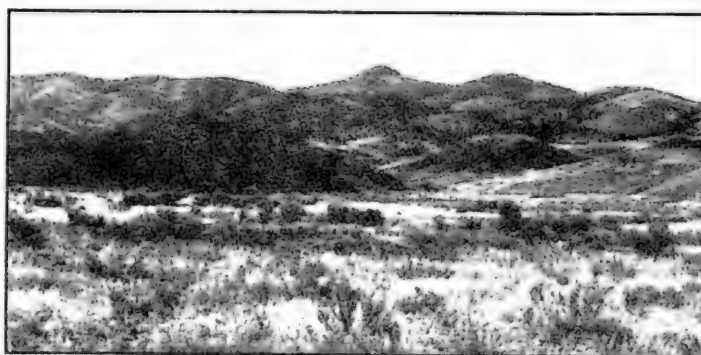
Eocene — Clarno Formation

The oldest rocks, about 40 million years old, found at Painted Hills are from the Eocene. These are from the Clarno Formation, named for the pioneer crossing over the John Day River at Clarno. This formation is a sequence of lava flows, mud flows and ash tuffs that are Late Eocene to Earliest Oligocene. Local tropical to sub-tropical conditions



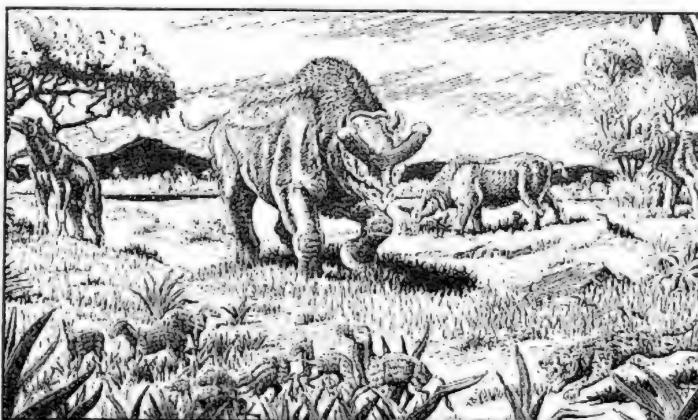
Black Butte, one source of Clarno Formation ash.

of 40 million years ago, as revealed by fossil flora, contrast sharply with today's arid environment. The present High Cascade Range was absent during deposition of the Clarno Formation. Warm, moisture-laden storms from the Pacific Ocean swept unimpeded across this part of what is now central Oregon. Up to 254 cm (100 in.) of rain may have fallen per year. The Pacific Ocean covered most of western Oregon. Today, parts of India may approximate the climate of 40 million years ago at what is now Painted Hills.



Bare hills of the John Day Formation, vegetated Clarno Formation hills beyond.

Through analysis of fossil nuts, fruits, seeds and leaves from other nearby fossil localities, we know that palms, tree ferns, avocados and catalpas grew here. Early horses, ancestral tapirs, primitive rhinos, crocodiles and oreodonts inhabited the lush forests. Volcanic ash from nearby active volcanoes (possibly White Butte and Black Butte to the



Eocene Mammals of Clarno time. Harold Comber Smith.

south) fell consistently in the region. This ash buried plant and animal remains and preserved them as fossils. The Eocene was a prelude to increasing volcanism to the west in what is now the Western Cascade Range.

Oligocene — The John Day Formation

Most landscape in the Painted Hills unit is composed of John Day Formation rocks and soils. Deposition of the John Day formation began about 34-36 million years ago. There were at least three sources for these strata: ancestral Cascade volcanoes, local eruptive centers and other volcanoes east of the current Cascade Range. Some eruptive centers may have been located near Powell Butte and Gray Butte to the west. These and other volcanoes spewed out light-colored rhyolitic ash high in silica (70%).

Products of these very explosive eruptions accumulated in the Painted Hills area as airfall and stream-carried material in lake and stream environments. These accumulations formed the cream-colored layers in the John Day Formation (Bishop 1989).

The Picture Gorge Ignimbrite is the 30.5 m. (100 ft.) thick ash flow sheet that caps Carroll Rim at Painted Hills.



Great Basin wildrye below Carroll Rim.

This particularly violent eruption spread super-heated, gaseous ash over a large area. It was hot enough to melt together the pumice fragments in it. The rim is in the middle of the John Day Formation with about 245 m. (800 ft.) of ash above it and almost 305 m. (1,000 ft.) deposited below it. The John Day Formation is sandwiched between the overlying Columbia River basalts and the underlying Clarno Formation.

The spectacular red hills at Painted Hills are part of the lower John Day Formation and are colored, in part, by iron oxides. The green colors may indicate the clay celadonite (blue), the zeolite clinoptilolite (yellow) or reduced iron. The buff colors are close to the original color of the ash. Almost all of these layers have been reworked and altered by pedogenic (soil-building) processes.

The Oligocene climate was warm-temperate and drier than that of Clarno times. The ancestral Cascade Mountains were then high enough to begin to exert their rain-shadow effect on lands to the east. Plant fossils from Painted Hills provide a good idea of local vegetation and climate 32 million years ago.



Painted Hills, Carroll Rim, with Sutton Mountain beyond.

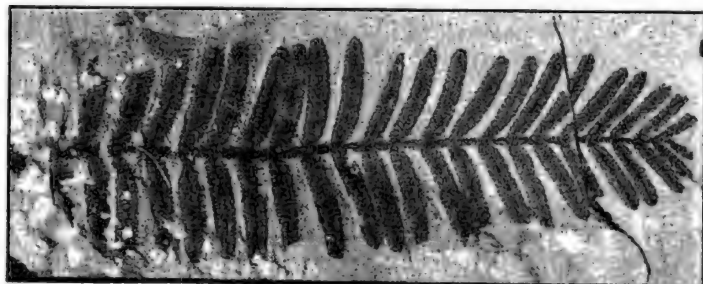


Bare John Day Formation Hills with Clarno Formation hills beyond.

The classic Bridge Creek fossil flora locality is at Painted Hills. Radiometric dating of the volcanic ash that buried the plants indicates these fossils are about 32 million year old. These plant fossil beds are somewhat below the strata where the best animal fossils are found (Manchester 1987). In some Bridge Creek shales, there are heavy concentrations of fossils with up to 210 fossil leaves per cubic foot of rock (Orr 1981). In 1883, Dr. John Strong Newberry published the first scientific descriptions of fossil plants from the John Day Formation. The Reverend Thomas Condon sent fossils collected at Painted Hills in the 1860's to Newberry, an experienced paleontologist and the first geologist on the faculty of Columbia University, New York City. He had traveled through central Oregon in 1855 as a geologist/botanist for the US Army's Williamson-Abbott Expedition which was part of the Pacific Railroad surveys (Garrett 1985).

Condon's and Newberry's work has been augmented by subsequent scientists. A picture has emerged of a temperate forest of deciduous hardwoods receiving up to 152 cm. (60 inches) of rain a year. The current forests of eastern Asia may approximate the Painted Hills forests of 32 mya. Alder (*Alnus*), Oregon grape (*Mahonia*) and oaks (*Hydrangea* and *Quercus*) were present. Eight species of maple (*Acer*) are found in the local fossil record. One of the extinct species was named *Acer ashwilli* after Melvin Ashwill, a noted paleontologist from Madras, Oregon. An extinct, five-needled pine is also present (Manchester 1987).

Original investigators identified coast redwood (*Sequoia*) from these strata. Subsequent researchers, however, named this taxon *Metasequoia*, a tree with deciduous, evergreen, opposite leaves, rather than the alternate, non-deciduous foliage of today's coastal redwood (*Sequoia sempervirens*). *Metasequoia* is referred to as the "dawn redwood." However, the title is misleading, because *Metasequoia* is not an ancestor to modern redwoods (Orr 1981). Although originally only known from fossils, *Metasequoia* was discovered growing in an isolated valley in Szechuan Province, China in 1947. This "living fossil" has been introduced into domestic cultivation.

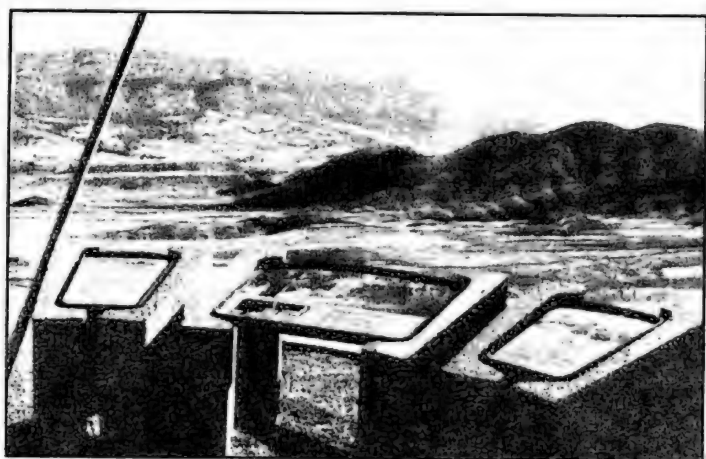


Metasequoia fossil.

Today, 15-20% of the fossil plant genera known from Painted Hills are globally extinct or are no longer found in central Oregon (Manchester 1987). The moist climate of Oligocene times contrasts markedly with the modern, dry climate. In these times, oreodonts, titanotheres, tapirs and early horses grazed under the forest canopy and on adjacent grasslands.

Middle Miocene — Picture Gorge Basalt

Absent from the Painted Hills Unit, but easily visible on the skyline east of Painted Hills.



View from Painted Hills overlook.

In the early Miocene, the rising Cascades caused a drop in rainfall to perhaps 76 cm. (30 in.). Forests were more temperate, with beech, birch, oak and chestnut replacing earlier forms. Saber-toothed tigers, cow-sized rhinos, miniature deer, oreodonts and intermediate horse forms lived in the forests and grasslands. During this time, about

16-12 mya, voluminous eruptions of relatively low silica (50%) basalt flows covered much of eastern Oregon and Washington, to depths of three miles. These are collectively referred to as the Columbia River basalts. Individual flows have been tracked for over 323 km. (200 mi.), and some even flowed in river canyons through the Cascades as intracanyon flows in the ancestral Columbia River, to the coast, forming some of the dramatic headlands there. Locally, the prominent Picture Gorge basalt flow erupted about 16-15.5 mya. In the Painted Hills Unit, these overlying flows eroded and are visible today only east across Bridge Creek Valley, where they make up the dark, imposing upper layers of Sutton Mountain.

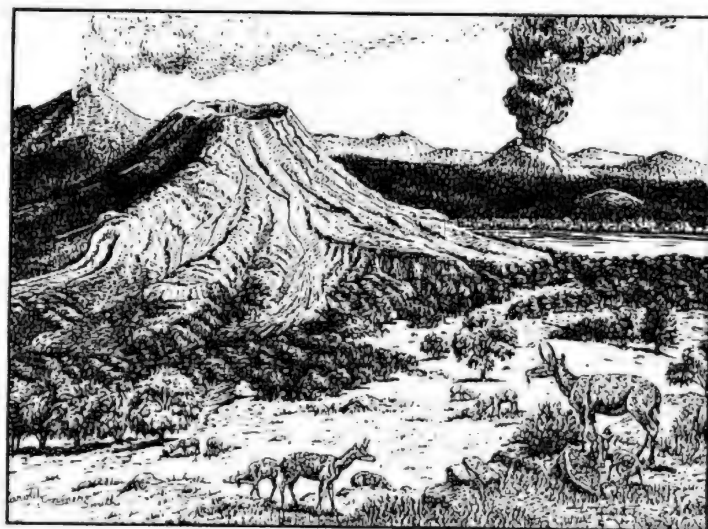
Late Miocene —

Mascall Formation 14 million years ago

Very Late Miocene —

Rattlesnake Formation 6 million years ago

Both of these formations, if they were present, have been eroded in the Painted Hills vicinity. They deserve mention because they tell an important part of the story of the increasingly arid climatic conditions that have led to today's vegetation in the region.



Eastern Oregon in the Mio-Pliocene. Harold Comber Smith.

To the east, the 14 mya Mascall Formation, composed mostly of tuffs, erupted at the close of Columbia River basalt volcanism. The Mascall Formation records a time of increasing aridity (but still moister than today), with some freshwater lakes. The area was inhabited by early deerlike antelope, horses, wolves and camels. Willow (*Salix* sp.), Ginkgo, aspen (*Populus*), cottonwood (*Populus* sp.) and fir (*Abies* sp.) grew in the area.

The even-younger Rattlesnake Formation (6 mya) records predominately grassland vegetation (with juniper and sage appearing), with more modern forms of the horse, antelope, camel and ground sloth present. Rhinoceroses, mastodons and peccaries grazed beneath scattered trees. This formation includes an ash-flow tuff ejected from a

huge caldera located near Burns. Remnants are found west to Smith Rock State Park and east to John Day and Seneca.

Modern Vegetation

Painted Hills lies in the Blue Mountain physiographic province of Franklin and Dyrness (1973). The first vegetation analysis of John Day Fossil Beds National Monument was conducted in 1976 by Berta Youtie and Al Winward for the National Park Cooperative Research Unit at Oregon State University. They mapped and quantified vegetation types and identified threatened and endangered plant species. Seven plant associations with communities in various seral stages and ecological conditions (as a result of grazing, fire suppression and agricultural practices) were identified at the Painted Hills Unit (Youtie and Winward 1977). The park is no longer grazed by domestic animals, and fire is being reintroduced, but recovery has been slow. Vegetation transects established in 1976 and resampled in 1989 showed a slight increase in perennial bunchgrass species (B. Kauffman, pers. comm.)

A description for each community follows. These community divisions may be considered as habitat types or plant associations of the shrub steppe, meadow-shrub steppe or juniper woodland zones.

Current Vegetation

Plant Associations:

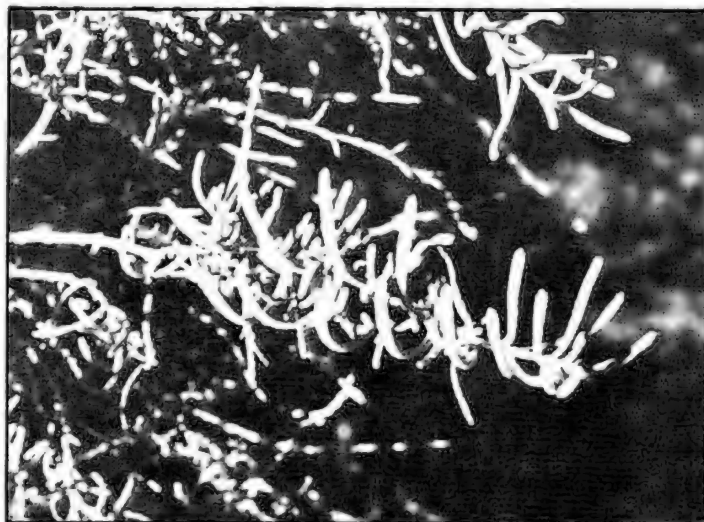
1. *Sarcobatus vermiculatus*/*Elymus cinereus* — *Distichlis stricta*
Greasewood/Great Basin wildrye — saltgrass



Greasewood and cheatgrass.

Greasewood is a large shrub that loses its thick, bright-green foliage in winter and is protected by sharp thorns. This vegetation type occurs in saline soils in bottomlands adjacent to Bridge Creek. Dominant understory species once included basin wildrye in the slightly-saline areas and saltgrass on the moderate- to highly-saline sites. Some flat, deep-soiled areas along the drainages may have supported nearly pure stands of basin wildrye or stands of big sagebrush/basin wildrye. Areas that traditionally supported

this vegetation have been farmed and heavily grazed. Exotic annuals such as cheatgrass (*Bromus tectorum*) and bulbous bluegrass (*Poa bulbosa*) now dominate the understory. It is believed that as Great Basin wildrye, one of the our largest species of native bunchgrasses, was reduced by wintering livestock and native hay production, greasewood density increased on these sites. However, there are no historical data to evaluate shrub density changes.



Black greasewood with succulent leaves and spines.

2. *Atriplex confertifolia*/*Poa sandbergii*
Shadscale saltbush/Sandberg's bluegrass

At Painted Hills, the sites that support this vegetation are on the alkali clays of weathered John Day Formation ash. Soil pH as high as 8.5 has been recorded. This vegetation type tolerates the edges of the John Day Formation habitat, which is generally devoid of all vegetation. Plants on these sites must tolerate high alkalinity and the shrink-swell properties of montmorillonite clay. Even weeds such as cheatgrass have a difficult time invading, although bluebunch wheatgrass and a greater diversity of perennial forbs may have inhabited these sites at one time.

Because these habitats are found at low elevations and close to water at Painted Hills, past livestock use may have been a major influence.

This vegetation type is more widespread in the salt-desert shrub zone of the Great Basin and is found only in a few areas in the Pacific Northwest. Shadscale saltbush appears as a medium-sized shrub with lateral branches forming sharp spines. Domestic animals and wild ungulate grazers utilize this shrub for winter forage.

3. *Artemisia tridentata*/*Agropyron spicatum* — *Poa sandbergii*
Big sagebrush/bluebunch wheatgrass — Sandberg's bluegrass

In much of the low elevation habitat of Painted Hills, the bluebunch wheatgrass component is no longer apparent. Snakeweed (*Xanthocephalum sarothrae*), a small half-shrub

resembling rabbitbrush (*Chrysothamnus* spp.), and annual forbs and grasses such as cheatgrass now dominate the understory. Sandberg's bluegrass has persisted under heavy grazing, while bluebunch wheatgrass has been nearly eliminated. At sites greater distances from livestock water, or on sites with steep topography, or more moist conditions due to higher elevation, the ecological condition improves. Bluebunch wheatgrass increases and big sagebrush cover decreases.

Big sagebrush is one of the icons of the desert west. It is remarkably well-adapted to its habitat. It has both shallow spreading roots and deep taproots to take advantage of available moisture. It sports long ephemeral leaves which appear early in the growing season and afford an early photosynthetic start by taking advantage of accessible spring moisture. Three subspecies inhabit Oregon; that at Painted Hills is subspecies *tridentata*.

4. *Juniperus occidentalis*/*Artemisia tridentata*/*Agropyron spicatum*
Western juniper/Big sagebrush/Bluebunch wheatgrass



Less than 50-year-old junipers invading big sage shrub steppe.

This vegetation type is very similar to the previous big sagebrush type with the addition of western juniper as the overstory component. Bluebunch wheatgrass is still present on some sites, although cheatgrass and Sandberg's bluegrass are dominant in lower seral stages. Idaho fescue (*Festuca idahoensis*) may also have been present in areas with a northern aspect.

At Painted Hills, junipers are found at higher elevations with stringers extending down the ravines. Junipers occur naturally on these sites, but have likely increased in density under the past management regime. Western juniper population expansion has been correlated with precipitation change in Pleistocene climatic conditions by Mehringer and Wigand (1984). Also, understory fuel reduction by livestock and suppression of wild fires by humans has allowed western juniper to invade adjacent areas (Burkhardt and Tisdale 1974).

5. *Artemisia rigida*/*Poa sandbergii*
Scabland sagebrush/Sandberg's bluegrass

One small site supporting this habitat type was found at Painted Hills. This vegetation type is quite common on

higher elevation scablands in the Columbia Basin and Blue Mountains. Scabland sagebrush is particularly well adapted to shallow, gravelly soils where its relatively deep taproot can extract moisture from cracks in the underlying bedrock. Also it is able to tolerate these xeric conditions by being drought-deciduous, dropping its leaves during the late summer months. Sandberg's bluegrass also has the ability to thrive in these shallow soils. The only other common species on this site is cheatgrass. Squirreltail grass (*Sitanion hystrix*) is a short-lived perennial bunchgrass often found in this habitat.

6. Riparian Vegetation

There is an intermittent spring east of Painted Hills Overlook with a diversity of hydrophytic plant species such as cattail (*Typha latifolia*), oatgrass (*Arrhenatherum elatus*), celery-leaved buttercup (*Ranunculus sceleratus*) and an array of rushes and sedges.

Recently, the BLM acquired the lands adjacent to Painted Hills along Bridge Creek. In 1976, there was only exposed, down-cut stream banks with no stabilizing woody vegetation. Today a major restoration project is underway to restore the riparian ecosystem along the creek. Through livestock exclusion, stream bank protection and planting of cottonwood, alder and willow, regeneration can be observed along the stream. Beaver dams are altering the hydrology of the area.

7. Mountain Brush Vegetation

Vegetation dominated by shrubs was identified on a talus slope adjacent to the scabland sagebrush/Sandberg's bluegrass site. Franklin and Dyrness (1973) referred to these shrub sites on talus slopes as shrub garlands. Western Serviceberry (*Amelanchier alnifolia*) and golden and wax currants (*Ribes aureum* and *R. cereum*) were the major species found and were present only at this location.

Endemic Species

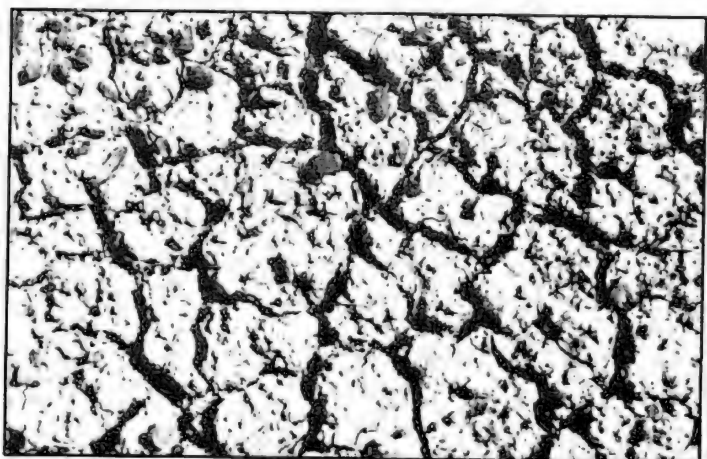
John Day Basin is home to several plants found nowhere else in the world. Native plants of restricted distribution are referred to as endemic. They may be endemic to a continent, a state, a particular mountain or even a single locality. Endemics are separated genetically from their ancestors by adaptations in response to differences in soil, climate, geographic isolation or a combination of these and other factors.

Cretaceous seas receded from central Oregon over 60 mya. Terrestrial plants have had a long period to establish themselves in this region. As noted, a number of species evolved, only to suffer extinction over geologic time. The series of cataclysmic volcanic eruptions in the Painted Hills area and climatic changes caused by the Cascadian rain-shadow undoubtedly influenced the species of plants found here. We know from the fossil record that many genera once growing here are gone from central Oregon (*Metasequoia*, *Platanus*, *Morus*, *Ulmus*, *Juglans*, etc.). Others are still represented in central Oregon (*Acer*, *Pinus*, *Mahonia*, *Abies*, *Rubus*, *Amelanchier*, etc.), if not actually at Painted Hills

(Manchester 1987). One aspect of Painted Hills is the fact that the area continues to support several plant species not found anywhere outside the John Day River Valley.

There are a number of reasons why the six locally endemic species discussed below have restricted ranges. Geographic isolation is one probable factor. Over the last 40 million years, a series of massive and destructive volcanic eruptions not only intermittently destroyed much local vegetation, but also made it difficult for other plants to immigrate into the area. Unlike the relatively small eruption of Mt. St. Helens (small, at least, on a global geologic scale), the Miocene basalts, the Picture Gorge ignimbrite or the Rattlesnake ignimbrite were orders of magnitude greater than the eruption of Mt. St. Helens, and would have totally destroyed all life in the areas where they were deposited. Obviously, this scale of eruption limits immigration of species from outside the destroyed area.

These endemic species grow in unusual soils. Some are paleosols, ancient soils which have been re-exposed, are rich in elements such as titanium and deficient in others, such as selenium. The roles of these factors in developing endemic plants of the John Day Valley have yet to be scientifically investigated. Physical characteristics of these soils are also unusual. Montmorillonite clay soils characteristic of the John Day Formation in Painted Hills have remarkable properties of expansion with hydration and contraction with drying. This gives the soils the so-called "popcorn" texture they exhibit in their dry state. This physical soil fluctuation makes germination and growth difficult for some plants. Expansion of the surface of these soils when rain falls tends to seal them and makes moisture penetration to deeper layers difficult.



John Day Formation clay.

Endemic Plant Species Found at Painted Hills

Liliaceae, many-flowered onion (*Allium pleianthum*). Flowering white to pink in April and May, this perennial onion is found only on the sticky, clay soils at low elevations. This taxon remains on the Oregon Natural Heritage Program review list due to the lack of information on its status as a sensitive species. This species is often confused

with Tolmie's onion (*A. tolmiei* var. *tolmiei*). The majority of occurrences are in Wheeler County between Mitchell and the Clarno Basin.

Fabaceae, John Day milkvetch (*Astragalus diaphanus* var. *diaphanus*). The small, biennial milkvetch with white flowers tinged with purple blooms in the spring. It has been collected from Grant County to the mouth of John Day River. It grows on very poorly developed soils and on scabland areas. This variety has recently been recognized as distinct from the var. *diurnus* growing on the south fork of John Day River, mainly due to fruit morphology.

Scrophulariaceae, John Day paintbrush (*Castilleja xanthotricha*). The common name of this taxon does an excellent job of describing the species. This yellow-flowered paintbrush is confined to John Day Valley and can be seen blooming from April through June in Wheeler County. It grows on the low elevation sagebrush-covered hills from river elevations to 765 meters. It is hemi-parasitic and grows in conjunction with sagebrush, snakeweed or bunchgrasses. In drought years, which are quite common in its range, this perennial paintbrush may be found in reduced populations.

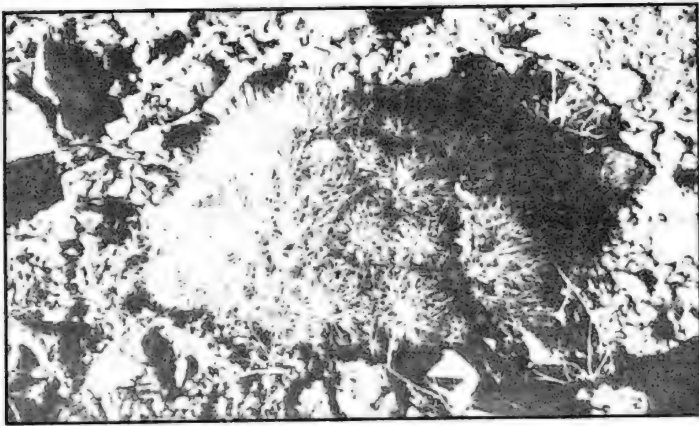
Asteraceae, John Day chaenactis (*Chaenactis nevii*). This yellow-flowered chaenactis is most often found in red clay soils of the John Day Formation in Wasco, Wheeler and Grant Counties, blooming in May and early June. The only yellow-flowered chaenactis in Oregon, this annual is very sensitive to moisture conditions. In relatively wet years, this species may grow profusely in small valleys among the red hills at the Painted Hills Unit. It is usually associated with golden cleome (*Cleome platycarpa*), another very unusual plant.

Scrophulariaceae, crested tongue penstemon (*Penstemon eriantherus* var. *argillosus*). This perennial penstemon is endemic to central Oregon and can be found blooming in June and July. It is locally common and seems to thrive on disturbed sites. Look for this species on road cuts.

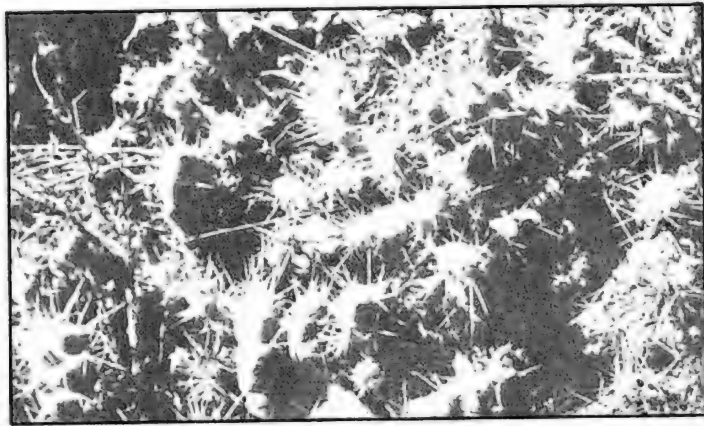
Rosaceae, belled cinquefoil (*Potentilla glandulosa* var. *campanulata*). This variety of perennial cinquefoil is characterized by petals that are erect instead of spreading and longer than the sepals as compared to other varieties. At Painted Hills, it inhabits rocky dry washes and blooms in May and June. It has also been collected on talus slopes and basalt cliffs in John Day Valley.

Other Interesting Species Found at Painted Hills

Cactaceae, hedgehog cactus (*Pediocactus simpsonii*). Although not endemic to John Day Valley, this barrel cactus can be observed in dry washes and rocky ridges at Painted Hills. It only occurs in a few places in Oregon. The cactus grows in clumps with flower shades ranging from yellow to pink to magenta, blooming from the end of April to the beginning of May. Another cactus, plains prickly pear (*Opuntia polyacantha*), is also found at Painted Hills but is more common throughout eastern Oregon.



Hedgehog cactus.



Prickly pear cactus.

Lamiaceae, purple desert sage (*Salvia dorrii*). This very fragrant shrub with blue-violet flowers and silvery herbage grows on barren hillsides in John Day Valley. When in bloom, these conspicuous shrubs can be identified from a long distance. The low-elevation, harsh sites are devoid of almost all other vegetation. Purple sage has a limited range within the Pacific Northwest.

Pallid milkweed (*Asclepias cryptoceras*). This species of milkweed is quite rare in John Day Valley. It is most often collected on the barren red clays of the John Day Formation. However, it has also been found on rocky clay sites with greater vegetative cover. The prostrate milkweed emerges on the hills in May from an enlarged, woody root. The inflorescence appears decumbent and almost artificial, as if someone had planted a plastic flower.

MANAGEMENT ISSUES

Fire

Fire has been a regular occurrence in the Painted Hills area, although no definitive data exist as to its frequency. The return frequency cycle probably ranged from a few years to a few decades. Fire probably occurred as a mosaic. Native Americans were known to use fire intentionally to enhance certain plant resources. There is no reason to

think they didn't do this in the Painted Hills area, but there is no documentation of such activities. Fire suppression has been practiced since Euro-American settlement. Suppression substantially changed the plant communities, favoring woody tree and shrub species over forbs and grasses. Recent prescribed burns on the monument demonstrate that grasses and forbs increase after burning, while juniper and sage decrease in burned areas.

Grazing

Perhaps no other land use in central Oregon generates more controversy than grazing. Perhaps no other use of the steppe has had the impact caused by grazing. Large numbers of Euro-Americans first traveled through the Bridge Creek area during the gold rushes of the 1860's. The first ranches were founded to provide beef for these miners. Native stands of grass were lush. The bottoms provided Great Basin wildrye and native hay. The uplands had intact stands of Idaho fescue (*Fescue idahoensis*) and bluebunch wheatgrass (*Agropyron spicata*). Early pioneer accounts refer to "grass up to the stirrups," or even to the saddlehorn.

When settlement occurred, large numbers of cattle, horses and sheep arrived in a relatively short time, perhaps 10 to 20 years. Large herds of livestock had been built up west of the Cascade Mountains, so stock no longer had to be trailed from California or the eastern states. It is inaccurate to place all the blame on the livestock industry for use and appropriation of all surface waters in central Oregon, the takeover by exotic species of much of our rangeland, dramatic increase in woody species and consequent decrease in grasses, and the severe alteration of riparian ecosystems and fisheries. However, the impacts of grazing have been significant and long-lasting. Current grazing practices attempt to avoid this damage, with the long-term goal of restoration of native plant communities on public land.

The most damage was probably done in the first few decades of grazing. By the 1920's and 30's, altered ecosystems showed impacted riparian areas, increased woody species and decreased native bunchgrasses. The general trend since then has stabilized or improved. It is remarkable how long it takes native grasslands to recover. In areas with heavy cheatgrass invasion, there is concern that original native vegetation can never be restored, or that cost of restoration will be prohibitive.

The Prineville District BLM, in conjunction with local ranchers, National Park Service and conservation groups, is working to reduce juniper, to reintroduce fire, to protect riparian areas and to enhance fish habitat.

Photos from Princeton Expedition of 1889 show substantial impacts in vegetation from grazing by that time — Princeton then and now.



Compare the 1889 Princeton University Paleontologic Expedition photograph of the Bridge Creek Valley (above) with the same scene in 1989. Notice the increase in juniper.



Exotics

One of the more alarming aspects of Painted Hills flora is the extent to which exotic plants have invaded the area. Cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kali*), knapweed (*Centaurea repens*), tumbling mustard (*Sisymbrium altissimum*) and whitetop (*Cardaria pubescens*) are all found in greater or lesser degrees in many parts of the park. Tall wheatgrass (*Agropyron elongatum*) has been seeded.

Cheatgrass is perhaps the most noticeable foreign invader. Introduced in the 1870's from Eurasia, it spread rapidly along rail lines. By 1900, it was well established in many parts of the west. Some accounts indicate that cheatgrass was intentionally brought in as an annual feed; others say it was introduced as a contaminant in hay or wheat, or was carried in by cattle from Eurasia.

In any event, it exists in nearly solid stands in some areas.

This is particularly evident on the lower hills west of Sutton Mountain along the east side of Bridge Creek. Cheatgrass, a winter annual, can germinate any month of the year, providing a competitive advantage over many native plants which are spring germinators. It grows during wet periods during winter, extracting necessary moisture from the soil. By the time native perennials germinate and begin growing in spring, moisture has been depleted. Cheatgrass also seems to tolerate fire well. It burns readily and reseeds vigorously following fire. Grazing doesn't seem to retard its spread. Some exclosures in eastern Washington still have the same dominant cover of cheatgrass that they had when fenced 50 years ago. Land managers have yet to figure out a way to restore native systems in the face of heavy cheatgrass infestation.

Riparian Issues and Restoration

Bridge Creek drainage suffers from degraded riparian areas due to poor grazing management during the last century. This has subsequently impacted the native runs of anadromous (salmon and steelhead) fish which inhabit John Day Valley, the largest undammed drainage in Oregon. Increases in woody upland species have increased soil loss and siltation. Spawning beds erode or silt over. Grazing in the riparian areas increases stream downcutting, destabilizes stream banks and decreases shading vegetation. Water temperatures are higher than anadromous fish can tolerate. Beavers have been reintroduced to Bridge Creek. Beaver dams and ponds are restoring an essential element of riparian communities. The future seems bright for this drainage.

Plant List

The following list of plants is selective rather than comprehensive. We have listed those plants which are dominant, likely to be observed or are of particular interest. Those who wish further information are referred to the work by Youtie and Winward (1977) for a complete list. Species listed here cover a variety of plant communities and include the most common and some rare species. Almost all of them can be seen along one or more of the trails listed below.

"RTE" indicates that this plant was or is on the Rare, Threatened or Endangered List for Oregon.

denotes a non-native species.

GRASSES: *Agopyron spicatum* (bluebunch wheatgrass); *Bromus rubens* (foxtail brome); *Bromus tectorum* (cheatgrass)#; *Elymus cinereus* (giant wildrye); *Festuca idahoensis* (Idaho fescue); *Sitanion hystrix* (squirreltail).

FORBS: *Achillea millefolium* (yarrow); *Agoseris hereophylla*; *Allium macrum* (onion), *A. tolmiei*, *A. pleianthium* (RTE); *Amsinckia tessellata* (fiddleneck); *Antennaria dimorpha* (pussytoes); *Astragalus diaphanus* (milkvetch) (RTE), *A. filipes*, *A. misellus*, *A. purshi*; *Blepharopappus scaber*; *Calochortus macrocarpus* (mariposa lily); *Cardaria pubescens*

(white top)#; *Castilleja chromosa*, *C. xanthotricha* (John Day paintbrush) (RTE); *Chaenactis nevii* (John Day chenaetis) (RTE); *Cirsium undulatum* (thistle); *Cleome platycarpa* (golden beeplant); *Crepis occidentalis*; *Crocidium multicauli* (spring gold); *Cryptantha celosioides* (cockscomb cryptantha); *Delphinium nuttallianum* (larkspur); *Draba verna* (whitlow-grass); *Erigeron linearis* (fleabane); *Erigonum sphaerocephalum* (rock buckwheat), *E. strictum*, *E. vimineum*; *Eriophyllum lanatum* (woolly sunflower); *Erodium cicutarium* (storksbill)#; *Erysimum asperum* (prairie rocket); *Fritillaria pudica* (yellowbells); *Helianthus nuttallii* (Nuttall's sunflower); *Lepidium perfoliatum* (pepperweed)#; *Lesquerella occidentalis* (western bladderpod); *Lewisia rediviva* (bitterroot); *Lithophragma bulbifera* (fringecup), *L. glabra*; *Lomatium hendersoni* (yellow biscuitroot), *L. macrocarpum* (white biscuitroot), *L. triternatum*, *Malva neglecta* (cheeseweed); *Microseris troximoides* (false agoseris); *Mimulus cusickii* (Cusick's monkeyflower), *M. guttatus*, *M. nanus*; *Oenothera tanacetifolia* (tansy-leaf primrose); *Opuntia polyacantha* (prickly pear cactus); *Pediocactus simpsonii* (hedgehog cactus) (RTE); *Penstemon erianthus* (figwort) (RTE); *Phacelia hastata* (waterleaf), *P. linearis*; *Potentilla glandulosa* var. *campanulata* (gland cinquefoil) (RTE); *Ranunculus glaberrimus* (buttercup), *R. testiculatus* (horned buttercup)#; *Salvia dorei* (purple sage); *Sedum lanceolatum*; *Sisymbrium altissimum* (Jim Hill tumblemustard)#; *Sphaeralcea coccinea* (globemallow); *Tragopogon dubius* (salsify)#; *Trifolium pratense* (red clover)#.

SHRUBS: *Amelanchier alnifolia* (western serviceberry); *Artemisia rigida* (scabland sage), *A. tridentata* (big sage); *Atriplex confertifolia* (shadscale), *A. spinosa* (spiny hopsage); *Chrysothamnus nauseosus* (gray rabbitbrush); *Ribes aureum* (golden currant), *R. cereum* (red currant); *Salsola kali* (Russian thistle)#; *Sarcobatus vermiculatus* (greasewood).

TREES: *Juniperus occidentalis* (juniper).

RIPARIAN: *Typha latifolia* (cattail).

Hikes

The National Park Service has a number of trails for visitors to Painted Hills. Remember that the National Monument was set aside to protect the paleontological and geological resources of John Day Valley. **Taking any of these resources is prohibited, and violators will be prosecuted.** The park encourages recreation such as hiking, wildlife viewing, plant observation and nature photography. Visitors are asked to stay on the trails. Here are several of our favorites.

Painted Hills Overlook Trail

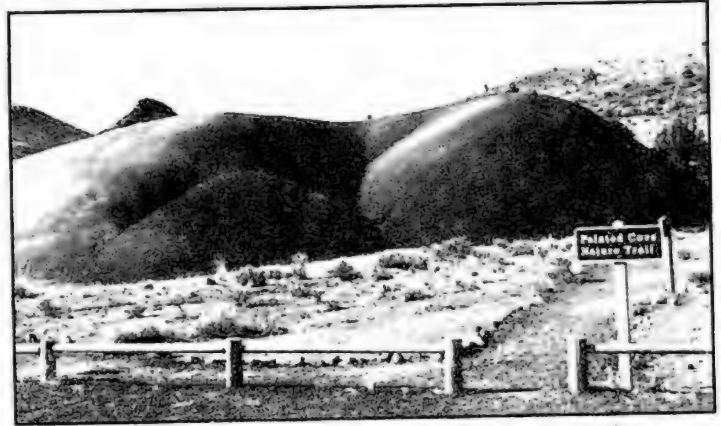
0.8 km. (0.5 mi.) one way

Start from the parking overlook for the hills. The red, gray, black, olive and tan of the hills are best early and late in the day. It traverses the big sagebrush/Sandberg's bluegrass community. John Day paintbrush is frequently seen in this area.

Carroll Rim Trail

1.2 km. (.75 mi.) one way

This highly-recommended short trail climbs steeply to the best overlook in the park. Sutton Mountain is to the east and the Bridge Creek Valley to the north. The north-facing slope near the top supports a stand of bluebunch wheatgrass that is in excellent ecologic condition due to its long distance from water and grazing. Nuttall's larkspur (*Delphinium nuttallianum*) is found growing in the talus at the summit.



Note tip of uncovered Oligocene hill in background.

Painted Cove Trail

0.4 km. (.25 mi.) loop

This short, easy trail winds through a small red hill formation. Interpretive displays are offered for the barren hills and other aspects of local geology. This is a good trail from which to see 30-million-year-old topography. There are two large Oligocene hills near here which have been uncovered by erosion and may represent original shapes (Fisher 1964). John Day chaenactis, bitterroot and golden cleome can be seen here.



Note dead junipers in prescribed burn in background.

Leaf Fossil Hills Trail

0.4 km. (.25 mi.) loop

Follow this trail to the type locality of the Bridge Creek

fossil flora where plant fossils were quarried from shale deposits. Big sagebrush, wheatgrass and juniper are found along the trail. Note the invasion of young junipers. The effects of a recent fire were still obvious in 1992. **No fossil collecting is permitted.**

Conclusion

In many ways, Painted Hills represents a microcosm of the plants and plant communities of central Oregon and the management challenges facing us. The complex history of human use of the area can be read in the changes on the land. How well we are able to restore these altered natural patterns will be judged by future generations.

Acknowledgements

The authors wish to thank Ted Fremd, National Park Service paleontologist; Ellen Morris Bishop, geologist; Ron Halvorsen, Prineville BLM and Ben Ladd, Superintendent of the John Day Fossil Beds National Monument, and Mel Ashwill, for reviewing aspects of this article. We accept full responsibility for any errors.

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— BOOK REVIEW —

Botanical Exploration of the Trans-Mississippi West, 1790-1850

By Susan Delano McKelvey, Oregon State University Press, pp1144, \$85

Frank Lang

The Arnold Arboretum of Harvard University originally published Susan Delano McKelvey's treasure trove of botanical history in 1955. Her careful work brought together information about the famous and not so famous botanical collectors of western North America from many widely dispersed sources. Although many accounts are abridged, the extensive bibliography gets you to the original sources.

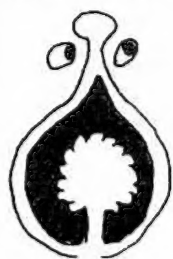
Until Oregon State University Press reprinted the book last year as part of its Northwest Reprint Series, it sold on the used-book market for as much as \$350, when available. The eminent botanical historian Joseph Ewan of the Missouri Botanical Garden wrote a foreword and added an updated, annotated bibliography. Stephen Dow Beckham of Lewis and Clark College wrote an introduction. Included are the nine original maps by Erwin Raisz and new color maps on the endsheets to show routes taken by the explorers discussed in the text.

Where else could you easily read about Archibald Menzies and the discovery of Madrone, *Arbutus menziesii*, or John

Kirk Townsend's account of a supper on the Nathaniel Weyth Expedition, September 1, 1834? From McKelvey's abridgement of Townsend's journal for that September day:

Having nothing prepared for dinner to-day, I strolled along the stream... and made a meal on rose buds... on returning, I was surprised to find Mr. N. and Captain T[hing] picking the last bones of a bird which they had cooked... the subject was an unfortunate owl which I had killed in the morning, and had intended to preserve, as a specimen. The temptation was too great to be resisted by the hungry Captain and naturalist, and the bird of wisdom lost the immortality which he might otherwise have acquired...

If you want to learn more: William Fraser Tolmie and Mount Rainier; or the German prince, Maximilian, botanizing the Missouri River; or how William Gamble met his end, McKelvey's **Botanical Exploration of the Trans-Mississippi West** is the book for you.



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